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THE TAXONOMIC VALUE OF THE ANTENNÆ OF THE LEPIDOPTERA.

A THESIS PRESENTED TO THE FACULTY OF CORNELL UNIVERSITY MAY 1, 1895, FOR THE DEGREE OF DOCTOR OF SCIENCE.

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TABLE OF CONTENTS.

INTRODUCTION.

The avowed aim of all modern classification in biological science is to group together those forms of life which have a close genetic relationship, and to show how they are related.

Though not always evident at first, there can be no doubt that community of descent affords the surest guide to similarity in the

greatest number of characters. Mr. Darwin* has called attention to the fact that, however unconsciously on the part of the systematist, descent has really entered into the classification in that no matter to what degree the two sexes may differ in the most important characters, they are placed together in the same most limited division, the species. The ideal natural system would consist of a complete genealogical table of all forms, exhibiting the phylogenies of groups and their subdivisions. There could be only one such perfect system, but it would admit of various expression. However far we are from its attainment, we may well be glad that a start has been made in the right direction. The attention of students is now being directed from the analytic to the synthetic aspect of the subject. From a dry, wearying process of sorting and pigeon-holing different forms for convenience in management, we have advanced to a study of their development and of the varying lines of descent through which they have attained their present condition—a study of great philosophic importance and of absorbing interest to the student.

In his "Evolution and Taxonomy,"† Professor Comstock suggests that "the logical way to go to work to determine the affinities of a group of organisms is first to endeavor to ascertain the structure of the primitive members of this group, and then endeavor to learn in what ways these primitive forms have been modified by natural selection, keeping in mind that in each generation those forms have survived whose parts were best fitted to perform their functions." He also suggests that the study be prosecuted by applying the method to a single organ; then to another, and so on till a consistent history is obtained. The essay gives his study of the evolution of the wings of insects, especially of the Lepidoptera, and presents a provisional system of classification based upon the results of that study. At the suggestion of Professor Comstock, and under his direction and encouragement, the present study of the antennæ has been undertaken.

The material for the work has been obtained largely from my own collecting in the vicinity of Ithaca, N. Y., and I have been allowed to avail myself freely of specimens from the extensive collection of the University. The slides of mounted antennæ of all specimens used in the morphological study are deposited in the University collection.

* The Origin of Species. New York, 1878, p. 372.

† Evolution and Taxonomy, Wilder Quarter-Century Book, Ithaca, N. Y., 1893, pp. 38-39.

I wish to acknowledge my great indebtedness to Professor Comstock for his constant readiness with suggestion and advice and for the invaluable assistance he has given me through his papers and by personal conversations. I am also under obligations to Mr. Alex. D. MacGillivray for the invariable kindness with which he has aided me in the work.

For morphological study the antennæ were removed from the head, and, after dehydration in 95 per cent. alcohol and subsequent immersion in clearer, mounted in Canada balsam. Each slide was labeled with the name of the species, sex, and the side from which the antenna was removed. The last item is of great importance, as it enables the observer to determine the relative aspects in the subsequent study.

For histological study the antennæ were removed with great care not to tear away the soft parts at the base. Some were fixed and hardened with parts of the head still attached. The chitin forms a dense covering over the softer parts, and it was possible to obtain better results in the fixing and hardening, and especially in the infiltration with collodion, if the antenna was first cut into moderate lengths so as to allow the fluids to work in from the ends. The tissues were fixed in various fluids. The Picro-aceto-sublimate, devised by Dr. P. A. Fish, gave the best results. It is composed of fifty per cent. alcohol, 1000cc.; glacial acetic acid, 5cc.; corrosive sublimate, 5 grams; picric acid, 1 gram. After immersion in this fixer for twenty-four hours, the tissues were passed through 50, 67, 82 and 95 per cent. alcohols and imbedded in collodion. The whole was cleared in the castor-thyme oil mixture*—red oil of thyme, three parts; castor oil, one part. Where extra thin sections were desirable, the cut surface was painted with one per cent. collodion before each section was made. This aided very materially in preventing the tearing away of the softer parts from the tough chitin. For staining, both Delafield's hematoxylin and the simple hematoxylin with a counter-stain of eosin produced excellent results.

After considerable study of the natural attitude of the antennæ in live specimens, both in flight and at rest, and also of the position taken when the insect is killed and spread, the conclusion has been reached that the normal position is assumed when the antennæ are extended directly laterad, with the most specialized surfaces ventrad,

* A New Clearer for Collodionized Objects, P. A. Fish, Proc. Am. Micr. Soc. vol. xv, pp. 86–89, 1893.

and the pectinations, where they exist, arising from the ventral surface. Some exceptions to the last clause will be noted later. This description of the normal position and Fig. 26, representing the denuded head and its appendages of *Sphinx chersis*, will make clear the application of the terms of position and direction employed in the following pages. The natural position varies greatly in different species. In some the antennæ are directed nearly cephalad; in others, almost as nearly caudad; and all the possible positions between these extremes may be assumed. As the antennæ are true appendages, however, the general rule for the normal position of appendages should obtain in all cases.

MORPHOLOGY.

The antennæ belong to the pre-oral somite, and are usually the most conspicuous pair of appendages of the head. They are slender, segmented organs, and are inserted symmetrically, one on each side of the meson, on the dorso-cephalic surface between or cephalad of the compound eyes. In the Papilionina and Hesperiina, according to Mr. Scudder,* and so far as I have observed, in the other Lepidoptera, the antennæ are inserted at the ends of the suture between the epicranium and the clypeus, see Fig. 26. Kolbe† says that, "In the Diptera, Lepidoptera and Trichoptera, whose mouth-parts are stunted, absent, or transformed into sucking organs, the antennæ are brought very near each other, while in the biting insects they usually are separated from each other." *Micropteryx*, one of the Jugatæ, which has retained its mouth-parts slightly modified, has its antennæ inserted quite far cephalad and relatively far apart; thus it offers a peculiar confirmation of the generalization of Kolbe. It would seem that, since the change in function of the mouth-parts has not yet become complete, as indicated by the presence of those organs in a condition less modified than in the other Lepidoptera, the migration of the bases of the antennæ has not progressed so far as elsewhere in the order. The insertions here are at the ends of the clypeal suture, but the suture itself is strongly curved with the ends bent cephalad.

The proximal segment of the antenna is the largest and is termed

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* The Butterflies of the Eastern United States and Canada, in three Vols., by S. H. Scudder, Cambridge, 1889, vol. i. p. 37.

† Einfuhrung in die Kenntnis der Insekten, von H. J. Kolbe. Berlin, 1893, p. 179.

the scape, Fig. 26. Next it is the pedicel, which is smaller than the scape, but larger than the segments immediately distad of it, except among some of the Hesperiina and Papilionina. The scape and pedicel together are often called the base, while all the remaining segments make up the clavola. Among the moths the latter is often pectinate, or feather-like, Fig. 3. There is much confusion in the nomenclature of this form, but in the following pages the general form will be termed pectinate; the part made up of the bodies of the segments, the shaft; and the projections, pectinations; Fig. 8, sh. and pe. Among the skippers and butterflies the clavola is divided into a proximal, thread-like portion, the funicle, or stalk; and a distal, fusiform, or clavate part, the club, Figs. 4 and 5.

The scape is inserted into a little cup-like depression of the head, and is itself more or less rounded in at the proximal end. Very often a constriction causes this end to take the shape of a spherical knob, which, with the corresponding cavity in which it fits, makes a very serviceable ball and socket joint. This permits great freedom of motion in many planes, and to a considerable extent provides for a rotary motion. The scape and pedicel also are joined in such a manner as to allow considerable movement. The other joints, however, are comparatively stiff and afford little or no motion.

HISTOLOGY.

The scape is abundantly supplied with strong, striated muscles, while in the other segments of all forms I have examined in sections, I have been unable to demonstrate the presence of muscular tissue. Fig. 20 represents a longisection of a segment with the two joints at the ends and shows the shape of the contiguous parts. The chitinous parts are held together by a tough, compact membrane, and it is due to the elasticity of the latter that, when the clavola is flexed by external force, it is able of itself to resume its natural shape. A section of this membrane is well shown in fig. 18, me. Figs. 20 and 22 will make clear the internal anatomy of the clavola. Just entad of the chitinous coat is a layer of varying thickness composed of dermal and nerve-cells with numerous interlacing nerve-fibres. Along the ventral part of the shaft runs a large tracheal trunk supplying the branches to the segments. Just dorsad of this trachea lie a pair of large nerves which come from the frontal ganglion and send out branches to the various organs of sense located in the antenna. The

remainder of the substance found in the interior is the blood, which freely bathes the tissues and provides for their nourishment.

The chitinous covering of the antennæ is of the same general character as that of the body, but it is neither so thick nor so compact in structure. It lies just ectad of the layer of dermal cells making up the limiting stratum of the vital tissues of the insect and is doubtless formed by the secretion from those cells. Its surface is frequently marked off into more or less nearly hexagonal areas, Fig. 34, which, in some cases, are said by various authorities to correspond to the underlying layers of cells. They are limited by very thin, continuous ridges of chitin sometimes, *e. g.* in *Notolophus leucostigma*, Fig. 30, raised as high as 3 *m.* from the surface. In other cases there is an external layer of overlapping plates which may or may not mark the outlines of the dermal cells, Figs. 38 and 39. The surface of the plates is often broken up into fine points and ridges which frequently obscure the outlines of the plates themselves. In still other forms there is a covering of fine hairs which are really simple projections of the chitin itself and quite different from the true hairs described below, Fig. 40.

The many structures found on the antennæ of the Lepidoptera which have originated from the interior may all be regarded as modifications of a simple hair. Each has its origin in a hypodermal cell, and therefore is connected with the interior through a pore-canal. The simplest form is that of a simple, protective hair, situated at the ectal end of a pore-canal. In the structure of the chitinized parts it differs slightly, if at all, from the sense-hair described later, but it lacks any connection with the vital tissues. Whether it is an imperfect form of sense-hair, or whether it is in the condition best adapted to the function it has to perform, is a question we are unable to answer.

A simple flattening out of a hair, followed by some corresponding changes in the secondary details of structure, would give the type of a scale. These also arise from a hypodermal cell, though in the imago the connection is lost. Fig. 16 shows the position and manner of insertion of the scales. The pedicel, or stalk, is set in a goblet shaped cell lying in the chitin with its long axis nearly perpendicular to the surface, but pointing slightly distad. The bottom of the cup is at the end of a pore-canal, but there is no evident vital connection with the interior. When the scale is extracted, or has fallen out, the insertion-cups have the appearance of two externally tangent, or

slightly overlapping circle, the distal one a little the larger. This manner of insertion differs considerably from that found in the wing-membrane and described by Professor Kellogg.* There the cups have their long axes nearly parallel with the surface, and they seem rather to be built up upon the membrane than to be hollowed out of it.

Scales vary greatly in form in different parts of the same antenna. The scape bears a patch of extremely long, little specialized scales spread over the dorsal surface towards the distal end and forming one or two very pronounced, often strongly colored tufts. Single scales of this kind attain great length, while their thickness remains small. One from the scape of a male *Hemileuca maia* measured 1888 x 5.2 *m*. Mr. Scudder says† that in the butterflies (by which term he includes the Hesperiina and Papilionina) the basal part of the base (*i e.*, the scape) is always naked. In many cases, however, these tufts cover at least the distal half of the scape; in some all the surface except that which forms a part of the joint. This tufting is carried to an extreme, or rather it is reinforced in a peculiar manner among the Epipaschiinæ. Here the length of the scales is supplemented by an extension of the dorsal surface of the scape into a long process, which in some species reaches nearly to the abdomen, Fig. 28. This is thickly clothed with long, spatulate scales, the whole forming a very prominent feature in the appearance of the insect. It is regarded by Mr. Hulst‡ as a secondary sexual development.

On the clavola the scales are more specialized, and have the same form as those on the wing of the same insect. Among the moths, for the most part, they are arranged on the dorsal surface in two transverse bands, the scales themselves lying with their long axes parallel with the axis of the clavola, and the free ends pointed distad, Fig. 49. Thus the scales of the distal band cover the joint between the segment on which they are born and the one succeeding. In many pectinate forms the pectinations also bear scales. Even in those antennæ which are scaled apparently over their whole surface, there is a comparatively free space on the ventral and more highly specialized face.

* The Taxonomic Value of the Scales of the Lepidoptera, V. L. Kellogg. Kansas Univ. Quar., vol. iii, No. 1, pp. 49-50.

† The Butterflies of the Eastern United States and Canada, p. 37.

‡ Entomologica Americana, vol. v, p. 44.

Of the various antennal organs which have a communication with nerves, and are therefore presumably organs of special sense, I shall describe six kinds:

1. Short, slender, pointed sense-hairs which are hollow, but closed at the free ends; Fig. 23, 1, shows these in their relation to the rest of the antenna; Fig. 13 represents a section magnified about 500 diameters. The hair is attached to the chitinous ring at the end of a pore-canal. It has been described as movably articulated, but there is no muscular tissue connected with it as with the hair of Mammals. The elasticity of the connecting zone of chitin may allow a certain amount of flexion and of subsequent extension, but it can scarcely be said to be movable in the active sense. In the specimens I have examined the external part of the hair does not exceed 45 *m.* in length, and it is usually more or less flexible. From the interior a fibre from a branch of the antennal nerve passes out into the cavity of the hair. Ruland* says the question whether the nerve, ascending through the pore-canal to a ganglional swelling, ends in the base; or whether it sends up a modified continuation into the interior, is not yet settled. He is unable to decide to his satisfaction. Some of my preparations seem to me to show clearly that the nerve itself extends some distance into the hair. Just entad of the hair lies a large nerve-cell. It is more or less ovate in form, with the smaller end produced into the pore-canal. It contains from three to six nuclei, which are coarsely granular in appearance. An "axis-cylinder" is clearly visible in the apical part of the cell, but it fades from sight toward the middle.

This type of sense-hair has a wide distribution. It occurs very generally in both the Jugatæ and the Frenatæ. Mr. Scudder† says that in no instance has he observed the antennæ of the butterflies clothed with hairs. He doubtless refers, however, to hairs of a different type described below. Those of the first kind are more or less abundant in many forms.

2. Long, very stout and rigid bristles or hairs, closed at the end; Fig. 14 represents a section of one from a male *Callosamia promethea.* These are easily recognizable by their thick base and tapering form, and also by their characteristic insertion. They have a distinct,

* Beitrage zur Kenntniss der Antennalen Sinnesorgane der Insekten, Franz Ruland, Hamburg. Zeitschrift fur wissenschaftliche Zoologie, vol. xlvi, pp. 602–628.

† Butterflies of Eastern United States and Canada, vol. i, p. 37.

compact ring surrounding the point of attachment and rising up around the base of the bristle. They vary greatly in size. They are usually shorter than the third type of sense-hair, but in some cases they are longer. In *Notolophus leucostigma*, Fig. 30, they measure 350 *m.* It is extremely difficult to obtain good sections of the soft parts of these sense-organs, because of the toughness of the chitinous parts, and the ease with which the cellular elements tear away from them in the cutting. As shown in Fig. 14, we have here more than one cell in connection with the sense-hair. I have been unable to determine whether all three are nerve-cells and receive branches from the nerve-trunk. That at least one is supplied with a nerve is certain. At a later date, with fresh material, I hope to devote further study to the histology of this form. Whether in all these cases the cell is really a nerve-cell and has true nerve processes, is a matter of doubt. Whether the nerve is really a part of the cell, or simply intimately connected with it by the apposition of a brush end has not been determined, and could perhaps be satisfactorily demonstrated only by the application of the Golgi method. Whichever condition may be the true one, however, it is doubtless constant in all forms, and so cannot affect the problem under consideration in this paper.

The distribution of the sense-hair of the second type is as wide as that of the first type, but the number is limited to a very few on a single segment.

3. Long, rather stout and stiff hairs which, like those first described, are hollow and closed at the free ends; Fig. 23, 3, shows these in relation to the rest of the antenna, and Fig. 12 represents a section of one from a male *Callosamia promethea*, magnified about 500 diameters. It will be seen from the figure that the structure differs but little from the first type. The nerve-cell, however, is relatively smaller, and the hair is more firmly attached. The external portion of the hair usually measures from 80 to 100 *m.* I have found none less than 75 *m.*, while some attain a length of 350 *m.* In distribution they are more limited than the other types. They do not occur in the Jugatæ, nor in the Hesperiina and Papilionina.

4. Pits, or depressions, guarded at the opening by stiff projections of chitin, and containing single rods or cones, which are connected with nerves from the interior; Fig. 15 represents a section of one from a male *Callosamia promethea.* In this species the pit is a depression in the chitin from 8 to 10 *m.* deep, and of about the same

diameter. Rising from the floor is a chitinous cone about 3 *m.* in diameter at the base and 6 *m.* high. The apex is somewhat attenuate and is open. The nervous apparatus is much like that in the first type of sense-hair. It is broader at the apical part and passes directly into the cone, filling the broad base. Sometimes two, or even three of these pits are grown together. In such cases there is a reduplication of all parts. Among the butterflies they are much deeper, and are supplied with stiff guarding projections from the walls, Fig. 17. The cone, also, is smaller in diameter at the base, and is almost or quite rod-like in form. In at least some cases, *e. g. Pyrameis cardui*, there is a circle of stiff points around the base of the cone. Hauser* describes such a bristle circle in *Vanessa io.* Kraepelin and Ruland,† however, from the study of different species, dispute the existence of such a structure. Pits have a wide distribution throughout the whole order. They are found for the most part on the ventral surfaces both of the shaft and of the pectinations. In the butterflies they are most numerous on the club. Hauser says they are not limited to the two terminal segments alone, as Lespes has declared, but are spread over the whole club. In *Vanessa atalanta* I have found them in all but the three proximal segments of the clavola.

5. Short projections which have become so thick as to lose their character of hairs, and which in many cases have a covering continuous with the general integument of the segments; Fig. 20, 5, represents the form of these cones and shows their relation to the segment. Fig. 18 represents a section of one from a male *Callosamia promethea.* The nerve apparatus resembles that of the rods in the pits described under 4. In fact the whole apparatus seems like an everted pit. The termination of the cone varies in different species. In some the end is blunt and even hollowed out; in others there is a fine point at the apex; in still others there are several points, Figs. 41–45. The distribution of the cones is wide. They occur in all the families of the Frenatæ, excepting the Hesperiina and Papilionina, and possibly the Pyromorphidæ. They are not found in the Jugatæ. Notwithstanding their broad distribution, there is usually only a single one on a segment, and in many cases only on the segments of the distal portion of the clavola.

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* Physiologische und histologische Untersuchtungen über das Geruchsorgander Insekten, Gustav Hauser, Erlangen. Zeit. fur wiss. Zool., vol. xxxiv, pp. 367–403 (1880).

† Antennalen Sinnesorgane. Zeit. fur wiss. Zool., vol. xlvi, pp. 602–628.

6. There is another set of nervous apparatus which, though it cannot afford any taxonomic characters, at least not without involving the careful preparation of difficult sections, may throw some light on the question of function. It is always situated in the pedicel. Fig. 19 represents a section through the apparatus in the antenna of a male *Callosamia promethea.* It is a sagittal section of the ventral half of the pedicel, with parts of the adjacent segments; but the apparatus extends around the whole segment, so that a longisection in any plane would present essentially the same appearance. As the antennal nerve-trunk enters the pedicel, it gives off on all sides numerous branches, which extend peripherad. When it approaches the outer wall each nerve bends distad and joins a nerve-cell with a distinct nucleus. Extending distad from the cell is a long, slender rod with one or more nucleal bodies. These rods are gathered into small conical bundles and terminate within pores situated in the membranous ring which connects the chitinized walls of the pedicel and the proximal joint of the clavola. It will be remembered that the base is the movable part of the antenna; while the clavola, except in case of the application of external force, is as one piece. It at once becomes evident that any movement of the clavola upon the base, whether due to its contact with some object or to a vibration caused by a vibration in the air, would be at once felt in the membrane in which these rods lie. As there are rods in every part of this membrane a definite impression of the movement would be produced in the sense-rods.

FUNCTION.

That the antennæ function as organs of special sense there can be no question. Just what the sense, or senses, may be, we cannot tell, but we may approximate the true character. When we consider how little we know of the essential operations which accompany our own perceptions, we must realize the difficulty of the problem. We can form definite ideas of what sensations are possible to insects mainly by interpretations of physiological action and of histological structure, as compared with similar actions and structures in ourselves and in the higher animals. Doubtless the range of perception in insects is widely different from our own; yet, that there must be considerable similarity in the organs, follows from the fact that the external substances or forces must work through the same media in both cases.

The senses which might be supposed to have their peripheral organs in the antennæ are touch, taste, smell, and hearing. The evidences of their existence we may class under two heads: histological and physiological, normal, and artificial or experimental.

Touch.—A very little observation will convince one that the antennæ are peculiarly sensitive to impressions of touch, and it seems very probable that the several types of sense-hairs already described are especially adapted to the receptions of such impressions. Blix* holds that in man all hairs are organs of touch, though at the same time they serve for protection. The sensation of pressure at least is closely associated with the hairs. In insects where the body is covered with a hard shell of chitin, we may fairly assume that the hairs are even more effective as intermediate organs between the external influence and the nerve termination. It is not at all improbable that the different types of hairs are receptive of different sorts of sensations, as of touch, pressure, weight, etc. The greater abundance of hairs in the nocturnal moths and their sparser distribution among the diurnal forms would seem to be correlated with their use as touch organs. One who has watched *Ctenucha virginica*, or some form of night-flying moth, will have little doubt that the antennæ serve as "feelers." It may not be impossible or even improbable that the sense of touch in these organs is not limited to conditions of actual contact with the objects perceived. Many phenomena connected with the actions of moths possessing these organs very highly developed point to the conclusion that there must be a sort of feeling at a distance such as we know of among some higher forms which are sightless.

Taste.—Histologically, we might suppose it possible that the pits and rods or the cones might function as organs of taste. Some authors hold that during life the pits may be filled with a mucous secretion. I do not think so, but if there were a fluid in them the apparatus would closely approximate the condition found to prevail in the taste organs of the higher animals. Experiments, however, have shown pretty conclusively that taste does not reside in the antennæ. It has been found that by the use of the antennæ wasps† could not distinguish powdered sugar from alum or dolomite, and only recognized the difference when some of the substance reached the mouth.

* Exper. Beitrage zur Losung der Frage über die Specif. Energie der Hautnerven. Zeit. fur Biologie, 1885.

† Das Geschmacksorgan der Insekten. F. Will. Zeit. fur wiss. Zoologie, 1885, p. 674.

Smell.—There can be little doubt that the sense of smell is very acute in the Lepidoptera. Hundreds of species of both moths and butterflies are known to possess special organs for the emission of odors. Dr. Fritz Muller* says that the males of *Didonis biblis*, one of the Nymphalidæ, is able to emit as many as three distinct odors, each kind being produced by a separate apparatus. The possession of contrivances for the emission of such odors would in itself argue the existence of organs for their detection. The wonderful celerity with which the Noctuidæ and Arctiidæ can find "sugar" at trees or in open places lends additional weight to the belief that there must be well-developed organs of smell. The only tenable theory to account for the well-known habit of "assembling" among Lepidoptera is based upon their possession of an extremely acute sense of smell or something very akin to it. This habit is not confined to any one group, though it is most frequently observed among the Saturniina. It has been noted† in many widely separated families, *e. g.*, Hepialidæ, Tortricina, Geometrina, Noctuina, Lymantriidæ, Lithosiidæ, Zygænidæ, etc. The most remarkable example that has come under my notice is recorded in "The Entomologist" of December, 1894. On the 19th of July, 1894, a gentleman of Carnforth, England, placed three females of *Bombyx quercus*, each in a cage of perforated zinc, in a leather collecting bag. On the 20th they were removed, and the bag was carried on a trip to the Isle of Man. On the 24th, after returning to England, the bag was taken to Witherslack Moss and a number of males not only came to it, but even crept inside. Afterwards, at various places, on the 26th, 27th, 29th and 31st, numbers of males came to the bag, *though no females had been in or near it since the 19th*, a period of *twelve days*.

During the early Summer of 1894, a breeding-cage with cocoons of *Callosamia promethea* was placed at one of the windows of the Entomological Laboratory at Cornell University. The window was a second story one, and was directly over a much frequented walk. When the warm days came the window was opened, and after females had emerged great numbers of males came to the cage, flying even in the middle of the day in strong sunlight. On the afternoon of the 15th of June, between three and half-past five o'clock, forty-

* Notes on Brazilian Entomology by Dr. Fritz Muller, Trans. Ent. Soc. London, 1878, pp. 211-223.

† The Entomologist. London, vol. xxv, pp. 84, 121, 163, 218; vol. xxvi, p. 21; vol. xxvii, p. 179.

six males flew into the laboratory and were captured. In all the cases I observed sight appeared to be of little use. The whole approach was made in a more or less indefinite manner, as if they were guided by the varying strength of the scent, and, even when the females were close to them and in plain sight, the males would still fly blindly about striking the sides of the building, and at last reaching the cage only after many wide detours. Dr. Westcott describes, in the "Entomological News" for May, 1895, his experience with *Cecropias*. In four days he took 342 males who came to a cage where females were confined. At one time he counted 218 about the cage at the same time, when it contained only four females.

Males of *Samia cecropia* have been known to anticipate the emergence of the female from the cocoon. In many forms where the female has lost her wings, or possesses them in a very rudimentary condition, she does not fly at all, or does so only to seek a place for depositing her eggs. As many as 183 species have been enumerated where the wings of the females are either greatly reduced or entirely absent. In these cases the males must seek the females, and observations show that they succeed in doing so in a wonderfully short space of time. These are certainly remarkable manifestations of some sense of perception, which, in many respects, must resemble our sense of smell. That the sense here concerned is not in any direct way connected with that of touch or with the sympathetic vibration of sense-hairs or organs, is proved by the example quoted above where the males were attracted to a bag from which the females had been removed for some time. The fact that "assembling" takes place among moths which have filiform antennæ also argues against the view that the pectinate forms by the vibration of their abundant hairs communicate at a distance.

There are many reasons why the pits and rods of the antennæ should be regarded as the peripheral organs of this sense. Histologically, there is much evidence in favor of the view. There is a supporting tissue with a perforated end, which would allow free communication between the air and the nerve or a thin protecting membrane, through which the perception may take place. The origin of the antennal nerve also presents some evidence that the sense of smell resides in the antennæ. Viallanes* says the antennal

* Etudes histologique et organologique sur les centres nerveux et les Organes des Sens des Animaux articules. Ann. de Sci. Nat. Zoologie, Huitieme Serie, T. 14. Paris, 1893. Ff. 405–456.

nerve is provided with two roots; one, ventral, composed exclusively of fibres affected by special sensibility, arises from the olfactory lobe; the other, dorsal, which includes at once motor fibres and fibres of general sensibility, arises from the dorsal lobe of the deutocerebron. Viallanes also shows the correlation between the development of nerve centres and their peripheral organs. In *Libellula*, whose eyes are so large, the optical ganglia acquire unusual dimensions; on the other hand, in the same insect whose antennæ are very small, the olfactory lobes become almost rudimentary. The reverse conditions prevail in ants.

The most plausible argument against the view that the organs of smell are in the antennæ is that stated by Mr. Arkle. He writes* as follows: "In animal organisms the gift of scent is exercised through the respiratory process. Lepidoptera possess this faculty beyond doubt, and, as the air inhaled is the carrying medium, we must look to the spiracles as the organs of smell." This opinion rests upon the assumption that the condition found in the higher vertebrates must also obtain in lower forms. I think this is a mistake. We, who, of all vertebrates excepting the Cetaceæ, have the most rudimentary olfactory lobes, can have little conception of the enormous range of perception, or of the mode of action of the sense of smell in the lower forms. That air is the carrying medium is doubtless true. Air, however, has access to the rods in the pits of the antennæ. The real question at issue, then, is whether a current of air such as would be produced by respiration is necessary, or whether the simple diffusion of the substance in the air would not reach the organs in the antennæ. That the latter condition is sufficient is evident when one considers the state of affairs in the lower vertebrates. Sharks have a highly developed sense of smell. Their olfactory nerves are of great size. Yet, there is probably little or no current of water over the olfactory membranes. In *Amia calva*, a Ganoid with large olfactory nerves, the nasal sac is not connected with the respiratory organs, the only communication with the outside being through a narrow tube opening at its free end above the surface of the head, and a small postnares. A number of different forms do not even have a postnares, *e. g.*, *Petromyzon marinus*. This must mean that a current of the carrying medium is not a necessary factor. The fact that the most careful preparations by skillful his-

* "The Entomologist." London, vol. xxvii, December, 1894, pp. 336–338. See also article by Watson in vol. xxviii, February, 1895, pp. 30–33.

tologists have failed to demonstrate any organs near the spiracles of insects which could be supposed to act as organs of smell, also lends argument against the idea of a current of air caused by respiration. Indeed, if the current is of any advantage, may it not be possible that the waving of the antenna so familiar to all observers would provide for it in sufficient degree.

Many experiments have been made upon insects to determine whether the antennæ are really scent organs. In most cases Coleoptera or Hymenoptera have been used because of their greater ease of manipulation. The most valuable experiments are those conducted by Hauser and described by him in the "Zeitschrift für wissenschaftliche Zoologie," Bd. 34. Auguste Forel* and Sir John Lubbock† have also performed many interesting and instructive experiments. These investigators believe that the sense of smell does reside in the antennæ. Some of them also believe that there may be other parts of the body or other organs which are sensitive to impressions of smell. Some experimenters have arrived at a contrary conclusion. Many of them, however, have in their tests made use of strong odors, often of irritating and corrosive substances, and, in consideration of the extreme delicacy of the sense being tested, it seems to me that their results are untrustworthy.

I have dwelt at such length upon the question of smell because its possession is of such great moment to the Lepidoptera not only in the detection of the whereabouts of their food, but in the more important problem of the perpetuation of their species. A review of all the arguments pro and con has forced the conviction upon me that the pits and rods, and probably the cones also, are the special organs of this sense. No other organs so well adapted are found in the insect and the number occurring in an antenna seems to be correlated with the importance of the use of scent in the life of the species. Hauser‡ says the bees and wasps have 14,000 to 15,000 cavities and about 200 cones in each antenna; the leaf wasps, a smaller number. The flesh and dirt flies have 60 to 150, while the flies that live on plants have only 5 or 6 to each feeler.

Hearing.—It is frequently denied that Lepidoptera possess the sense of hearing, and evidently they pay little attention to the ordi-

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* Experiences et remarques critiques sur les sensations des Insectes, Recueil Zool. Suisse, T. 4, 1886.

† On the Instincts and Senses of Animals.

‡ Popular Science Monthly, vol. xxiii, p. 284.

nary sounds which are sensible to our ears. It does not follow, however, that they do not hear sounds of which we are not cognizant. Dr. H. Landois* gives an account of sound-producing organs among insects and describes sounds produced by eleven species of Lepidoptera with which he experimented. In many cases the sounds were weak, but he says the weakness of the tones of many was due partly to the lightness of the sound, partly also to its being of such a nature that it cannot be perceived by human ears. The senses of touch and hearing are doubtless very intimately connected. That the antennal hairs of certain Diptera are auditory organs has been pretty clearly demonstrated, and it is not at all improbable that the antennal hairs of the Lepidoptera may be of some use for the detection of sound. The set of apparatus described under section 6 seems especially adapted to the perception of any sort of delicate pulsations of sound waves. C. M. Child† has described this apparatus, which he terms "Johnston's Organ," as found in the Culicidæ and Chironomidæ, where it has a remarkable development. He believes that its functions as an organ for the perception of both touch and sound, and that the insect is able to distinguish between the two sensations by whether any resistance is offered to the free movement of the antenna.

EVOLUTION OF THE ANTENNÆ.

In the preceding chapter I have described the general form and structure of the antennæ of the Lepidoptera. I have also endeavored to indicate the character of the organs found upon them and to arrive at some conclusions regarding their function. In the present chapter I shall point out what I believe to be the primitive form of Lepidopterous antenna, and to indicate in a partial manner the paths by which the evolution of the more specialized forms has taken place.

The most generalized form of antenna of existing Lepidoptera so far as I have been able to examine specimens is to be found in the genus *Micropteryx*. The genus contains two distinct types, but *M. semipurpurella* may stand as the representative of the one which

* Die Ton- und Stimm-apparate der Insekten in anatomisch-physiologischen und akustischen Beziehung. Zeit. f. w. Zool. Bd. 17, pp. 105–186.

† Ein bisher wenig beachtete antennales Sinnesorgan der Insekten, mit besonder Berucksichtigung der Culiciden und Chirononomiden. Zeit. f. w. Zool. Bd. 38, 1894, pp. 475–528.

retains in the fullest degree the characters of the stem form. Fig. 1 exhibits the general outline of the entire antenna, and Fig. 53 a single segment more highly magnified, showing the finer structure. It will be noticed that the scape is differentiated from the other segments by its larger size and different shape; that the pedicel is not very different from the proximal segments of the clavola, but the whole base is easily distinguished from the other parts by its covering of very generalized scales. These are like long hairs, while those which make a dense covering over the whole clavola are comparatively specialized, being broad with emarginate apices. The simple, cylindrical segments which compose the clavola show little variation from the common shape and present almost no projections or asymmetrical expansions of the body wall. There are numerous hairs of the first type, especially on the ventral aspect of the distal segments, and a few of the second type. The latter are limited to one, or at most two, on the ventro-distal edge of the segments, and a considerable number in various positions on the apical segment. Other characters appear in the antenna, but for our present purpose those named are the important ones, as indicating what we may fairly predicate of the stem form of the Lepidoptera. We may say, then, that the primitive antenna of the Lepidoptera was made up of a scape large enough to afford room for the strong muscles to provide for the movement of the pedicel, and also to contain the large trunks of tracheæ and nerves which supply the parts distad; of a pedicel large enough to provide space for the nervous apparatus described under section 6 of the preceding chapter; of a clavola composed of numerous segments, probably at least a score, all of them very much alike. What was the character of the chitinous surface we cannot say. Doubtless there were hairs of the first type. There may have already been specialized hairs of the second type.

In the evolution of any complex organ, natural selection has acted upon the different component parts and many lines of specialization may have progressed together. This is true of the antennæ, and in considering them we must necessarily treat of different features separately. The most striking changes are those of general shape. The variations of the scape and pedicel are for the most part within narrow limits and are in the direction of changes in their size relatively to that of the clavola, and in the varying proportions of length and thickness. The scape has undergone modification in two directions according as one or the other of its functions has been of predomi-

nate importance in the action of the antenna. When exact and definite movement became of greater moment, the tendency was towards an increase in diameter and relative shortening of the length. This would provide for a much more advantageous arrangement of the musculature, both as to the direction of the axis of the fibres and the securing of a better leverage for their operation. This line of specialization has reached its climax in the Hesperiina and Papilionina. On the other hand, when the direct movement became of less importance than the separation of the two clavolas and the ability to move them from two distinct and widely separated bases somewhat removed from the head, then selection caused a lengthening of the scape accompanied by little increase in diameter. This line of specialization has progressed quite far in certain of the Microfrenatæ, especially among the Tineina.

The pedicel shows but little variation among the moths. In the more specialized families it is of greater size, relatively to that of the adjacent segments of the clavola, than would be necessary, did it serve simply as a socket whose function was to hold the clavola, while the pedicel itself might be moved by the muscles situated in the scape. It is very probable that the degree of its development is closely correlated with that of the contained nervous apparatus already described.

The greatest variation occurs in the clavola. This is the part which more directly bears the sense organs, and therefore is peculiarly subject to the action of natural selection. We may safely assume that the primitive form of the segments of the clavola was cylindrical, with the whole surface equally provided with hairs, the latter uniting in their function protection and sense-perception. When there came the differentiating modifications of the hairs into different types, and the consequent differentiation of the surfaces of the clavola, the organs specialized for sense-perception came to be more or less localized on the ventral aspect, while those for protection were concentrated on the dorsal. It at once becomes evident that, if the chief function of the antenna is sense-perception, specialization would be in the direction either of enlarging that part which bears the sense organs and thereby providing for an increase in their number and spread, or of increasing the efficiency of the organs themselves. As a matter of fact, both processes went on together.

The extent of the ventral surface was enlarged by progress along

two different lines of specialization. In one there was a projection of the surface ventrad, resulting in a form of antenna in which the line of the joints appears to be thrown out from the line of centers of the segments, and is at the dorsal side of the shaft, Fig. 47. When carried very far this projection is emphasized on the mesal line and a distinct ventral ridge is formed. In the other line of specialization, instead of a ventral expansion, there is a sudden projection of a small portion of the segment at the ventro-distal edge forming a flattened expansion whose lateral edges are produced into the more or less slender prolongations which we call pectinations.

The evolution wrought in the shape of the segments by the earlier and simpler method is a very gradual one. The most generalized forms, *e. g. Micropteryx semipurpurella*, see Fig. 1, shows a slight tendency towards the increased development of the ventral surface. In the Microfrenatæ the development is carried further. Here we invariably find a considerable enlargement, but the surface is usually more or less rounded off. *Pyrausta oxydalis*, Fig. 47, will afford an illustration of what I mean. The stage of the formation of a distinct ventral ridge is best shown in such forms as *Crambus mutabilis*, Fig. 21, where the ridge is thin and attains a width equal to twice the diameter of the shaft proper. This same extreme development is also found among the Sphingidæ, Fig. 46.

The second kind of specialization has undergone a more complex evolution. There can be little doubt that the pectinations arose, perhaps after the first kind of specialization had progressed to a certain extent, as simple extensions of the ventro-distal edges of the segments. The antennæ of the females of those species of which the males have highly specialized pectinate antennæ often afford an insight into the probable successive stages through which the forms have attained their high development. The most instructive series for this study can be found among the Saturniina. All the males of the Citheroniidæ and Saturnidæ have two pairs of pectinations to a segment for at least a portion of the clavolas, while in only a few genera of the Saturnidæ do the females have them. In most cases the females have non-pectinate antennæ or have only a single pair of pectinations to a segment. Whether they have simply lagged behind the males in the process of specialization, or have degenerated from a common form, it is difficult to say. Mr. Poulton* believes

* The external Morphology of the Lepidopterous Pupa; its Relation to that of the other Stages and to the Origin and History of Metamorphosis.—Part IV, by Edward B. Poulton. Trans. Linn. Soc., London, second series, vol. v, Zoology, pp. 246–

that all such cases of sexual inequality have been gradually reached by a degeneration of one sex attended by a corresponding development of the other, and that a tendency towards such an action arose whenever the females were less active than the males. His chief argument for this theory is that the antennal cases of the pupæ are practically alike in both sexes and are larger and more complex than the adult antennæ of the female would warrant, though at the same time less developed than the adult male antennæ. A different explanation, however, may be offered. In these families oviposition takes place very soon after the emergence of the female from the cocoon and neither the male nor female adults seek food to prolong their existence. Their mouth-parts have been lost or have ceased to be functional. If this habit of early oviposition was acquired before the antennæ had time to develop very far, it is plain that there would be little tendency in either male or female to attain better antennæ for aid in the search for food. At the same time the struggle of the males to find the females quickly would cause a sudden and extreme specialization of their antennæ, without a corresponding influence upon the female. Darwin has pointed out that "peculiarities appearing in the males of our domestic breeds are often transmitted either exclusively, or in a much greater degree in the males alone." This would seem the more natural explanation of the condition we find among the Lepidoptera. It is so common to find the female with antennæ much less developed, that it is difficult to believe that they all have degenerated from a form intermediate between the present male and female antennæ. It is a much simpler and reasonable explanation and one which is as fully in accord with the facts to believe that in the large majority of cases the females have simply not kept pace with the males in the specialization of their antennæ.

Whichever may be the true explanation, the comparative study of the series is equally instructive. Degeneration is apt to retrace the steps by which the form was specialized, and so affords nearly as good illustrations of intermediate stages as would the real progressive series.

Another suggestive series is afforded by the gradation of the pectinations on the different portions of the same antenna. The medial and proximal parts show the more advanced stages, while the distal retains the earlier and simpler ones; see the gradation in *Feltia subgothica*, Figs. 9, 11, 10. This, however, is not true in the case of those organs which find their most favorable situation at the distal end.

From a comparative study of these corresponding forms in the two sexes and of a large series of male antennæ, I conclude that the evolution of the pectinations was essentially as follows: A single pair of pectinations originated on the ventro-distal edge of the segment. As development went on there was a steady selection of those forms in which the pectinations had their origin less toward the extreme distal end. The result was that the bases of the pectinations gradually migrated proximad. In addition to this movement there was also a tendency towards a migration dorsad. This last was a slower and a later method of specialization, but one which more directly resulted in an increase of the sensitive ventral surface. Among the Saturniina we find a further development. Here, with the exception of the Bombycidæ proper, we find the pectinations are dorsal, and where they have largely developed and have migrated to the extreme proximal ends of the segments, a second pair have originated as outgrowths from the distal edge of one segment towards the overshadowing pectinations of the proximal edge of the adjacent segment. The earlier form of this is seen in *Automeris io*, Fig. 8, where the distal pair of one segment is so closely apposed to the larger proximal pair of the next, that it is difficult to see the line of junction except with a considerable magnification. In *Tropœa luna* the distal pair have begun to migrate proximad and have become independent of the older and more firmly established ones. In *Samia cecropia* the two pairs of each segment are more nearly equal throughout the clavola, while in *Philosamia cynthia*, Fig. 3, the distal pair have migrated so far proximad as to occupy almost the middle of the segment.

We have seen how natural selection has caused an increase in the area and spread of the sensitive surface. Along with this process there was a differentiation of the hair structures themselves, and doubtless a corresponding increase in their efficiency. It is probable that in the primitive form of antenna a differentiation had already taken place between hairs for protection and for sense-perception. The simplest form of the latter sort has already been described as a hair of the first type. A comparative study of types two and three will show that, while they are quite distinct from the first and from each other, no great change would be necessary to transform the first into either the second or third. Intermediate forms do not exist in the same antenna, but different species show different degrees of variation from the first type.

The long, stout, rigid hair of the second type arose very early, before the separation of the Jugatæ from the Frenatæ, and long before the third type originated. The latter type was developed subsequent to another division which took place after the separation of the Jugatæ from the Frenatæ, and also after the Hesperiina and Papilionina had branched off from the Frenate stem. It departs less widely from the first type, and it is evidently specialized as a touch organ. It reaches its highest development among the Noctuidæ, Lymantriidæ and Arctiidæ.

At first sight the pits are very different from the simple sense-hair. Nevertheless, I believe that in essential characters they differ from them much less than do the hairs of the second type. The antennæ of a female *Epargyreus tityrus* will show that in many of the pits hairs very like those of the first type occupy the place of the short rods found in the more highly developed pits, and different specimens will present various stages of transition from the hair in a comparatively slight pit to a short rod in a deeper one. This shows that the structure is not yet definitely fixed in character, and that it may vary greatly in a short time.

The cones are a distinct development, however, and in all probability originated but once. This must have been after the separation of the Jugatæ and the Frenatæ, and also after the Hesperiina and Papilionina had branched off from the latter. All the Frenatæ, except these two superfamilies and possibly the Pyromorphidæ, possess these organs. They are quite constant in location. In all of the Microfrenatæ, and in most of the Macrofrenatæ, they are distributed one to a segment as shown in Figs. 46-50, and they form a very conspicuous feature of the antenna. In some of the Macrofrenatæ, however, they number more than one to a segment, and in pectinate antennæ they have often migrated from the shaft to a position upon the pectinations. Fig. 25 represents a portion of the ventral aspect of the antenna of *Phryganidea californica* where the cones still occcupy a position on the shaft. Fig. 27, representing a portion of the right antenna of a male *Zeuzera pyrini*, shows this migration with the cones situated part way toward the distal ends of the pectinations. Fig. 30 shows a portion of a pectination of the antenna of a male *Notolophus leucostigma* with the cone at the extreme distal end. Among the Saturnidæ, the number of cones to a segment is greatly increased. Fig. 7 represents a distal portion of the antenna of a female *Tropœa luna* with clusters of cones in the

same position usually occupied by the single one. It is perhaps worth noting here that, while the females are usually behind the males in the development of pectinations, they are not at all deficient in the number or the perfection of the cones.

There is yet another feature which is of importance in determining the relationship of an antenna. This is the character of the surface of the chitinous exoskeleton of the clavola. In the Jugatæ the surface as a whole is even, but has numerous slender prolongations which have received the name of fixed hairs, Figs. 51 and 53. These are not articulated with the chitin as are the true hairs. They are simply points which are continuous with and parts of the general surface and do not originate at the ends of pore canals. In the Frenatæ these are not found, but the surface of the whole clavola is divided up into more or less hexagonal areas bounded by thin continuous plates set normal to the surface, or into a series of more or less imbricated plates with various surfaces and outlines. These two distinct kinds of surface covering are of great importance, as they represent specializations differing in kind, and therefore indicate a dichotomous division in the line of descent. There are other characters which would indicate the same thing, but no other antennal character shows that the Hesperiina and Papilionina branched off from the other Frenatæ after their separation from the Jugatæ. The degrees of specialization attained in this character of surface are also worthy of attention as they sometimes afford clues to the real positions of families.

The surface marking of the chitin of the clavola in the Frenatæ presents a great variety of forms, but with the possible exception of a few apparently aberrant cases it is possible to trace a pretty definite line of development passing through them all. This is important, because it means that the system originated but once. The simplest and probably the most primitive condition exists in the antennæ of the Pyralidina. Here we find the general surface smooth, but divided up into more or less hexagonal areas, fenced off as it were by continuous plates of chitin standing normal to the surface. The areas thus demarcated are said by some authorities to correspond with the outlines of the underlying dermal cells, and it may be that the plates represent the edges of separate areas of chitin developed from the cells as centres. In the adult condition of most forms, however, I do not believe that the arrangement has any relation to the underlying structures. Fig. 34 represents a portion of the an-

tennal surface of a male *Pyrausta oxydalis*, and shows the great regularity of the areas so characteristic of this group of moths. Among the Tortricidæ we find that in most cases the areas become elongated. Fig. 35, a portion of the antenna of a male *Dichelia sulfureana*, shows this condition. This elongation of the areas is carried much farther among the Tineids. *Tinea dorsistrigella*, Fig. 36, shows this extreme lengthening of cells and straightening out of the cross-lines; yet here we still find the plates continuous. The function of these plates is doubtless to strengthen the thin layer of chitin and give it greater rigidity. In those forms which have long slender pectinations we find the longitudinal plates much thicker and heavier, while the transverse ones are less developed and have a tendency to straighten out or to disappear. This is evidently better adapted than the hexagonal arrangement to stiffen these slender forms. Fig. 30 represents the dorsal aspect of a pectination of a male *Notolophus leucostigma*, and shows at the sides some of the plates in profile, while the accentuation of the longitudinal plates is clearly seen in the middle of the figure. Note also that the longitudinal plates extend slightly beyond the end of the pectination. One cannot help being struck with the resemblance between the striæ or ribs of the scales and these thicker ridges on the chitin surface. On the ventral aspect of the same pectination we find a modification somewhat different, but yet along the same line. The abundance of the sense-hairs and the other organs makes a lighter and more delicate surface desirable, and here the transverse plates are either wanting entirely or transformed into longitudinal ones. In fact, we may state it as a general rule that the development of chitin on the ventral and sensitive surface is not carried so far as elsewhere. Fig. 31 represents this condition. In all these forms the general surface is approximately level and the plates represent the only elevations from the surface. Now we come to another development. Fig. 32 represents a portion of the dorsal surface of the antenna of a male *Automeris io;* ab is the mesal line of the shaft, and the part to the left is the extension of the surface upon the pectination. It will be seen that the portion near the meson resembles the condition found in *Notolophus leucostigma*, with this difference however: in *Automeris io* the general surface, instead of being level, rises on one side of each plate so as to make each area constitute a single slope with its crest at the plate on the distal edge. The surface of the sloping area is divided up into ridges with what was originally a transverse plate

at the crest of each ridge. These ridges when greatly developed extend beyond the apex of the slope and give the whole an appearance of being covered with fine points. This modification may be carried to an extreme. *Cerura cinerea*, represented in Fig. 37, will show an unusual degree of development in this direction. As a rule, however, the plates are smaller and more uniform, and form a regular imbricated surface, such as is found in *Hemileuca maia* or *Papilio polyxenes*, Figs. 38 and 39.

In a smaller number of cases the surface rises to the plates on each side, making a double slope, with the plate at the crest. This may be illustrated in the antenna of *Daremma undulosa*, Fig. 33.

As might be expected, the extent to which these surface modifications of the structure of the chitin is carried depends largely upon the development of scales. Where the antenna is heavily clothed, we find usually less departure from the primitive form of surface, especially if the scales are closely and compactly arranged. In most cases the surface of the scape and pedicel is practically smooth. This is doubtless in consequence of the covering of thick tufts of long slender scales, and also because the abundant scales of the vertex of the head afford it sufficient protection.

DISCUSSION OF FAMILIES.

This chapter will contain a discussion of the antennæ of Lepidoptera by families, or groups of families, as the case may be, and will give my interpretations of the evidences they present, which may be of taxonomic value. In this discussion the provisional classification of Professor Comstock will be followed, because it is the one with which I am most familiar and because I believe it represents the true relationships better than any other.* The characterizations of groups quoted in the following pages are taken from the "Manual." It would be presumptuous for me to propose any changes in the classification, but where the evidence of the antennal structures is contrary to that of the wings, note will be made of such contradictions as indicating the need of further study of the group. To be complete, a classification must take into account all the structures found in the body, and it was for the purpose of adding the evidence of one more organ that the present work was undertaken. In most of those species where the antennæ of the males and females differ

* Manual for the Study of Insects. John Henry Comstock and Anna Botsford Comstock, Comstock Pub. Co., Ithaca, N. Y., 1895.

markedly in the degree of specialization both sexes have been studied, but in the tables and descriptions which follow reference is always made to the conditions found in the males, unless special mention is made that the case is otherwise.

JUGATÆ.

The suborder Jugatæ was established by Professor Comstock, and was based principally upon important characters in some of the wing structures which represent specializations differing in kind from those of analogous structures in insects of the other suborder.* This division of the order into the Jugatæ and Frenatæ represents the earliest dichotomous division of the stem form of the Lepidoptera. The antennal character which distinguishes between the two lines of descent is the presence in the first of fixed-hairs upon the surface of the clavola; and in the second, of plates or their modifications. Professor Kellogg has already pointed out that the Jugatæ possess fixed hairs upon the wing-membranes; and he regards them as an example of a "persistence of a primitive wing-covering, probably represented in the wing-covering of the living Trichoptera." It may be added that he believes their absence among the Frenatæ is due to a disappearance. I believe that the system of fixed hairs is a distinct kind of specialization, closely resembling that found in the Trichoptera and also in the Diptera and Hymenoptera; while the system of plates with its later developments is just as distinct and differs from the first. If this is so, it indicates that the Jugatæ are more closely related to the Trichoptera than to the Frenatæ; that the stem form passed down in two lines of descent, and that the Frenatæ represent one, while the Jugatæ and the Trichoptera represent subsequent divisions of the other. This conclusion would really mean that the Jugatæ are Trichoptera rather than Lepidoptera. It may at first sight seem that the character of the surface covering is a trivial one and not worthy of so much attention. Darwin, however, laid it down as a geneaal rule that "the less any part of an organization is concerned with special habits, the more important it becomes for classification." We may recall in this connection that certain features apparently of little physiological importance often afford the most reliable characters. This is especially true of surface covering, *e. g.* hair of Mammals, feathers of Birds, scales of Reptiles, etc.

* The Descent of the Lepidoptera. J. H. Comstock, Proc. Am. Ass. Adv. Sc. vol. xli, 1892, pp. 199-200.

There are other reasons for considering the Jugatæ closely allied to the Trichoptera. The possession of a jugum, the branched condition of radius of the hind wings, and some other characters of the venation, the condition of the mouth-parts in *Micropteryx*, all point to the same conclusion. In view of all these indications, it may at least be regarded as an open question whether the Jugatæ are true Lepidoptera.

Another antennal character for the suborders is the absence of cones in the Jugatæ and their presence in the Frenatæ. The cones form a conspicuous feature of the antennæ of nearly all Frenatæ. The only exceptions known to me are the family Pyromorphidæ and the superfamilies Hesperiina and Papilionina. The antennæ of the Pyromorphidæ, however, are all pectinate, and those of the Hesperiina and Papilionina are so peculiarly specialized as to be easily recognizable. The presence or absence of cones, therefore, is a practical recognition character.

The suborder Jugatæ includes two families, the Hepialidæ and the Micropterygidæ, and each is represented in North America by a single genus.

The HEPIALIDÆ.—The members of this family have very generalized antennæ. Their size as compared with that of the body of the insect is extremely small. At the same time they present some evidences that a degeneration has lately taken place, or is even now in progress. Fig. 2 represents the antenna of a female *Hepialus argentata*. The lack of regularity in the segments of the clavola and the incompleteness of the joints would seem to indicate that the character of the segmentation has not yet had time to become fixed, or that it is now in the process of evolution. The fixed hairs are very numerous, and are somewhat stouter relatively than those in *Micropteryx*. Correlated with this abundance of hairs there are few scales. These are inserted along the dorsal aspect of the proximal part of the clavola. The scape and pedicel are large, and are pretty thickly clothed with long scales over nearly their whole surface. The clavolas vary considerably in the number of segments. Thirty-one is the largest number in any of the specimens in the University collection. The ventral expansion of the shaft is inappreciable, and there are no pectinations in any of the forms I have seen. Sense-hairs of the first type are numerous, and there are several of the second type to a segment. Pits are present, but vary greatly in their distribution. *H. argentata* has few; *H. mcglashani* has many, though they are not very highly organized.

The MICROPTERYGIDÆ.—The members of this family have the most generalized antennæ of any of the living Lepidoptera. As has been already noted, I find two types of antenna in the same genus. *Micropteryx semipurpurella* has already been described somewhat at length in the chapter on the evolution of the antennæ, and may stand as a representative of the simpler type. It is so generalized in structure that I can find in it no character which would distinguish it from some of the Trichoptera. Compare it with *Mystacides nigra*, and the striking resemblance in structural characters will be evident. Nor is the resemblance superficial only. The clothing of scales is practically alike in form and arrangement, the same organs exist in both. The only appreciable difference is in the number and relative length of the segments, neither of which characters can be regarded as of any great taxonomic value among the Lepidoptera. The second type exhibits a remarkable peculiarity in the arrangement of the scales. Most of them are gathered into two radiating tufts and have their origin in two circular or oval depressions, one on each side of the distal half of the segment. This is a unique specialization, and I have no idea of its purpose. Fig. 51 represents a segment of the antenna of a male *Micropteryx seppela* (?) and shows this arrangement of scales. *M. purpurella* has the same arrangement on a much smaller scale, and other species vary between these extremes. Another indication of the higher specialization of this type is the presence of very broad, short scales on the scape and pedicel in addition to the ordinary covering of long narrow ones. There are also numerous long curved sense-hairs of the second type which form a sort of pointed sheath around the segment and give it the appearance of that of *Anabolia bimaculata*, one of the Trichoptera.

A comparison of the antennæ of the Hepialidæ and Micropterygidæ will show that those of the former family are more highly specialized. Aside from the specialization in the scales just noted, the antennæ of the Micropterygidæ are very primitive. Pits and rods do occur, but in no case have I been able to find more than a single one to a segment, while in the Hepialidæ there are often many. The nearly naked surface of the clavola in *Hepialus* must also be regarded as an indication of a higher type.

FRENATÆ.

The suborder Frenatæ is divided by Professor Comstock into two principal sections: the Generalized Frenatæ, including those fami-

lies which "are supposed to retain more nearly than any other Frenatæ the form of the primitive Frenatæ, those that were the first to appear on earth," and the Specialized Frenatæ, including those "that depart more widely from the primitive type of Lepidoptera, being more highly modified for special conditions of existence." The first group is a small one and comprises only five families, none of which are large.

The Generalized Frenatæ.

I believe the evidences of the antennæ of this group agree with those of the wings as given by Professor Comstock. The five families represent lower branches from the primitive stem, and so have a bond of connection in that none of them have departed very widely from the primitive type. While the evidence is not conclusive enough to show that any two of the families are genetically related, except through the common stem, there are some indications in the structure of the antennæ that the Megalopygidæ and Eucleidæ are more closely connected than any other two families; while the Pyromorphidæ seem to represent a perfectly distinct line of descent. It is evident that if each of these families represents a distinct line of development, the group as a whole will be a homogeneous one only in the sense of containing those forms which are very generalized, and that is the character of the group as given by Professor Comstock. That there is a wide difference between the degree of specialization attained by the members of these families and those of any others is quite certain. I do not think any one familiar with various forms of antennæ would fail to pick out those belonging to this group. The extent to which the scape and pedicel are clothed with scales; the method of insertion of the scales more or less obliquely to the surface, and the irregularity in their arrangement; the scarcity of pits in most forms and the simplicity of their structure; the very slight extent of the ventral expansion of the segments; all are characters which, though perhaps not so constant in all cases as to permit of exact definition of limits, will yet enable one to distinguish these families without much difficulty.

The Megalopygidæ.—The members of this family have very generalized antennæ. The segments are short and numerous. *Megalopyga crispata* has sixty-one composing the clavola. The pectinations arise from the extreme ventral aspect of the shaft and the bases of each pair are closely apposed. They are long and well pro-

vided on the ventral surface with sense-hairs of the third type. An indication of the generalized condition of the antenna is the covering of scales over the whole dorsal surface of both the shaft and the pectinations. The base is covered with long, narrow scales, forming a prominent tuft on the dorsal aspect. On the shaft the scales are little more than flattened hairs. Indeed, for some distance from the insertion-cups they are cylindrical in form, and they are very narrow throughout their length. They are relatively long and stand out obliquely from the surface. These scales are broader and more specialized than some on the wings and other parts of the body, but they show the form characteristic of the family, narrow and lightly pigmented. There is a very small number of both pits and cones, and they are located on the pectinations. The pits are very rudimentary in structure, and, excepting in the possession of a short rod, depart but slightly from the first type of sense-hair. Where the cones appear at all, they have migrated to the extreme distal ends of the pectinations and project from the ends in the midst of the more or less crowded growth of scales.

The PSYCHIDÆ.—The females of all the Psychidæ remain in their larval sacs even in the adult state, and they have become wingless. The males, however, fly, and are compelled to seek the females in their cases before pairing can take place. As might be expected from such conditions, we find the antennæ quite highly developed in certain directions; yet as a whole they are of a very generalized type. As in the Megalopygidæ, nearly the whole surface of the scape and pedicel is covered with long, narrow, hair-like scales, and all of the clavola excepting the ventral aspect is clothed with scales of but little higher type. The greatest development is reached in the pectinations. Relatively, they are the longest found among the Lepidoptera. In *Psyche confederata* some of those near the middle of the clavola attain a length equal to one-half that of the whole antenna. The bases of the pectinations have migrated proximad and occupy a central position on the segments. Hairs of the third type are numerous on the ventral surface of both shaft and pectinations. They are well developed, but have no regular arrangement in their insertion. Pits are rare, and are limited in the forms I have studied to the two or three distal pairs of pectinations. Cones also are rare, and when present are situated at the ends of the pectinations. The antennæ of *Theridopteryx ephemeræformis* present a peculiarity in the joint between the scape and the pedicel. The latter segment is

jointed, not at the apex of the scape in the ordinary way, but is set obliquely on the caudal edge of the apex.

The COSSIDÆ.—The members of this family have well-developed antennæ. The shaft is stout and strongly chitinized. The pectinations are well developed in the males, and in some of the females. The base is clothed with short, broad scales, with rounded or emarginate apices, and with numerous very narrow scales of greater length scattered among the broader ones. On the clavola there are very few scales, and these are confined to the dorsal aspect of the shaft, and even there are quite closely applied to the surface. This is doubtless correlated with the habit of swift flight of these insects, and resembles in this respect the condition so characteristic of such swift fliers as the Sphingidæ. In the Cossidæ, however, the insertion of the scales is not so regular. The pectinations are well supplied over their whole surface with sense-hairs of the third type. They are more abundant, however, on the ventral aspect. The pectinations arise from the ventral aspect of the shaft, but a curious development in *Zeuzera pyrini* gives them the appearance of having migrated dorsad as in some of the highly specialized forms. A transverse, elevated, rounded ridge connects the bases of the pectinations of each segment and causes them to appear as a single continuous growth, joined to the shaft at right-angles. *Prionoxystus robiniæ* presents an unusual arrangement of depressions containing sense-hairs. They lie just dorsad of the bases of the pectinations and extend out for a certain distance upon them. There is a considerable variability in this family in the supply of cones. *Zeuzera pyrini* has as many as two on some of the segments, while *Prionoxystus robiniæ* has only an occasional one. In none of the species are the cones highly developed.

The EUCLEIDÆ.—The antennæ of members of this family present in some respects an unusual condition. Regarded as a whole, they are as generalized as any of the Frenatæ, but they possess cones which show a considerable degree of development. The base is almost entirely clothed with long, narrow scales mingled with many shorter and broader ones. In *Euclea querceti* every part of the surface is covered. The clavola, also, is closely covered, except on the ventral aspect, with broader scales, which, by their loose and irregular manner of insertion, indicate a very low degree of specialization. In *Lymacodes Y-inversa* even the ventral surface of the shaft bears numerous scales. In the pectinate forms the pectinations are heavily

clothed, even to their distal ends, where the scales from three sides unite to form a thick tuft extending beyond the end. The pectinations are ventral, and at or near the distal edge of the segments. *Euclea querceti* is peculiar in having the pectinations of the cephalic side of the antennæ flattened and nearly as broad as the length of the segments, of which they form a part. We find in the Eucleidæ an unexpected development of cones. They are long and slender, and are often several pointed at the apex as in the Megalopygidæ, Fig. 43. Some species have several to a segment. In the pectinate forms the cones have migrated to the apices of the pectinations, where they are protected by the thick tufts of scales before mentioned. Pits are very rare, seldom more than one or two to a segment, and then only on a few segments. I have been unable to find any in *Euclea querceti.*

The antennæ of the Eucleidæ differ markedly from those of the Cossidæ and Psychidæ. Though not supplied with numerous sense-hairs of the second type, they resemble the antennæ of the Megalopygidæ quite closely. A similarity of the surface covering; of the character of the cones; and, where they occur, of the pits also, indicate a relationship between the two.

The PYROMORPHIDÆ.—The Pyromorphidæ have a characteristic form of antenna which can be easily recognized. The segments of the clavola are not enlarged towards their distal ends, and in some forms are even gradually contracted near the joints. The pectinations are comparatively short, are cylindrical and almost clavate in form, and are contracted at their bases where they meet the shaft, so much so that they appear to be articulated with it. The base is thickly clothed with broad, deeply emarginate scales, and the dorsal and lateral surfaces of the shaft and pectinations of the clavola also are covered with a thick coat of scales arranged irregularly. On the pectinations the surface of the chitin is divided into a series of irregular imbricated plates with their surfaces broken up into points which give the appearance of longitudinal striations. Both the chitin and the scales are quite heavily pigmented with dark brown or black, and this in addition to the irregularity of the surface makes it difficult to see as clearly as desirable. I have been unable to find any cones in these forms, but am not at all certain that they do not occur. Pits are present, and are broad and shallow, with convex bottoms and short, pointed rods rising from their rounded apices. Hairs of the first type are particularly abundant, and there are a few of the second.

The Specialized Frenatæ.

The Specialized Frenatæ are divided into two groups: the Microfrenatæ and the Macrofrenatæ. The Microfrenatæ include those moths in which "the anal area of the hind wings is not reduced, having usually three anal veins, except in certain minute forms where a broad fringe has been substituted for the membrane of this area." The group comprises the superfamilies Pyralidina, Tortricina, Tineina and the family Sesiidæ. The antennæ of the members of this group, with the exception of the Sesiidæ, are quite constant in structure, and can generally be separated from any other Lepidoptera with great ease. The only forms which might cause any difficulty are among the Geometrina in the family Sterrhidæ. The separation of certain species of the genus *Acidalia* from the Microfrenatæ will require some experience on the part of the analyst, nevertheless the antennæ of the Microfrenatæ, with the exception noted above, indicate that the group is a definite one.

We are unable to find constant structural characters in the antennæ which are peculiar to the several families constituting the group. There are characters, however, which throw much light upon their relationships. The antenna of a *Pyrausta oxydalis* may be taken as typical of the Pyralidina. The clavola is long, slender and filiform, composed of many segments all of which are quite similar. Where there is any dissimilarity, the segments of the proximal portion are not so specialized for the increase of the sensitive surface, but are better adapted for the support of the distal portion. Fig. 47 represents a typical segment. The arrangement of scales, the position of the cones, the pits with their conspicuous circle of guarding points, the ventral expansion of the segments, all are features practically constant in the whole superfamily; in fact, with little modification of some parts, they are constant in all three superfamilies. The constant and peculiar character of the three superfamilies, however, is the division of the chitin surface into areas by thin plates normal to the surface. The peculiarity of the condition in the Microfrenatæ is that, however the shape of the included areas may be varied, the bounding plates are continuous, and the general surface remains even, see Figs. 34, 35 and 36. As already stated, I believe the different shaped areas are all modifications of the hexagonal form and represent differences in degree only, not in kind; yet as a rule, the limits of each superfamily are sufficiently separated

in degree to make the use of this character practicable in taxonomic work. The hexagonal form is characteristic of the Pyralidina, see Fig. 34. Among the Tortricina the lengthening process has begun, and the form shown in Fig. 35 is characteristic. Even where little elongation has taken place, the areas are much more irregular, and many of them have sharp angles in their outlines, which are not found among the Pyralidina. In the Tineina the process has been carried much farther and the form shown in Fig. 36 is characteristic. So far as I have examined, none of the Pyralidina has areas of the second or third form; none of the Tortricina has areas of the third form. The only liability of error in the use of this as a recognition character is due to the fact that in a few forms a heavy coating of scales has retarded the progress of the development, and we may find a Tortricid with a surface like a Pyralid, or possibly a Tineid with a surface like a Tortricid or a Pyralid. These cases, however, are rare, and where they do occur, there is usually some other character, such as the long, clavate scape so common among the Tineids, which will make it possible to separate the forms. There are many variations in the antennæ of the Microfrenatæ. The peculiar modification of segments and scales near the middle of the clavola of the male *Desmia funeralis*, Fig. 29, the crest of scales along the base of the clavola of the male *Laodamia fusca*, and of certain of the Tineids, the strange, tufted, membranous expansion of the scape among the Epipaschiinæ, Fig. 28, are examples of some of these variations, but the main structural characters remain the same even in these forms.

There are a few points of structure in connection with some of the families of this group which are worthy of mention. Among the Crambidæ, the ventral expansion is greater than in the other families. It reaches an extreme in *Crambus mutabilis*, Fig. 21, and resembles the form so common among the Sphingidæ. The antennæ of the Pterophoridæ and the Orneodidæ show a wide difference in their structure. Those of the former family are distinctly of the Pyralid type, while the latter are just as distinctly of the Tineid type. I believe a further study of the characters of other organs will prove the Orneodidæ to be more closely related to the Tineids than to either the Pyralids or the Tortricids. The surface marking is Tineid in form, and the scape has the long and slightly clavate shape so common among the Tineids.

The antennæ of the Sesiidæ, which we have excepted from the statements made of the Microfrenatæ, are distinctly different in

structural features and in general appearance from all others of the group. Mr. Butler* expressed the view that the Sesiidæ in their antennal characters are closely allied to the Pyralids and Tineids, and not at all to the Sphinxes, especially to the genus *Hemaris*. He believes that they should be placed between the Pyralids and the Tineids. Every feature he mentions, however, as characteristic of the Sesiidæ, and not found in the genus *Hemaris* can be paralleled in the Sphingidæ, even in the genus *Hemaris*. *Hemaris bombyliformis* was used by him for the comparison. I have not seen that species, but *Hemaris thysbe* presents the very characters he describes and figures in *Sphecia*, except that in both cases the "pencil of rigid hairs" is really composed of rigid scales. Lord Walsingham has already pointed out that Mr. Butler was mistaken in his description of the similarity of structures in the Tineids and Sesiids; and we cannot adopt the view that the antennæ indicate that the proper position of the Sesiids is between the Pyralids and the Tineids. The close resemblance in structure and form in the antennæ of the Sesiids and the Sphinxes certainly points to a genetic relationship. The large, compressed ventral expansion, the fusiform or clavate shape, the peculiar distribution of sense-hairs of the third type, the relative size, development, and position of the cones, the tuft of long, slender, rigid scales, projecting from the distal segment, the character of the chitin surface, are all features common to both the Sesiids and Sphinxes, and no other forms known to me possess the whole combination of characters. The condition of the Sesiids' antennæ is less highly specialized than we find it among the Sphinges; the specialization does not differ materially in extent from that of the other Microfrenatæ, but it has proceeded further in certain directions; so, while the family is properly classed with the Microfrenatæ, I believe it at the same time represents an offshoot of the branch which later on gave rise to the Sphingidæ. Figs. 49 and 46 represent segments of the clavolas of *Sannina exitiosa* and *Daremma undulosa*. Note that the arrangement of the sense-hairs of the third type on the wide, compressed, ventral expansion in *Sannina* is further developed in *Daremma* till there is a large semicircle, within which there are sense-organs.

There is of course a possibility that the great similarity of appearance, and even of structure of an organ may arise from similarity in environment and in the conditions of life, but in the case of the

* Trans. Ent. Soc. London, 1878, p. 121.

Sesiids and Sphinxes the resemblances are more than superficial; they are as marked in the microscopic as in the macroscopic characters, and it is difficult to believe that such forms could arise unless there was some genetic relationship.

The Specialized Macrofrenatæ.

The Specialized Macrofrenatæ includes "certain moths and all skippers and butterflies. In these insects the anal area of the hind wing is reduced, containing only one or two anal veins." This division is again divided into two subdivisions: the Frenulum-conservers and the Frenulum-losers. The first subdivision contains those moths in which the frenulum has been retained, while the second contains forms "in which the frenulum has been supplanted by a greatly extended humeral area of the hind wings." In a few members of the first group we find no frenulum, but it has evidently been lost late in the life of the species, as closely allied specialized forms still retain it. "Among the Frenulum-losers," on the other hand, "the loss of the frenulum occurs while the race is still in a very generalized condition, no trace of a frenulum being found among these insects, except a rudiment in the most generalized forms (*Bombyx*, *Cicinnus*)." Thus the two subdivisions really represent two distinct lines of descent which separated far back in the history of the races, and are not simply arbitrary groups based on the presence or absence of a single character, as has been understood by some authors.

The Frenulum-conservers.—Among the frenulum-conservers we find moths with highly specialized antennæ From the very fact of their great development we might fairly expect to find considerable variation even in small groups; and such is the case. A feature which is characteristic of the whole group is the specialized condition of the chitinous surface of the clavola. The perpendicular planes on the surface are not everywhere continuous, and usually the general surface slopes up to the top of the plane on one side and presents an appearance such as is represented in Figs. 37 or 33. In the filiform antennæ of each family there is not so much difficulty in finding characteristic structures, but when the highly pectinate forms are studied the problem becomes more difficult. The greatest variation occurs among the Geometrina. There we find some forms scarcely more specialized than many of the Microfrenatæ; and others, as highly specialized as any of the Frenulum-conservers. The following table will serve to separate the antennæ of this group

as far as I have been able to study them, and, unless it be among some of the Geometrina, I believe it will be found to hold for all the forms of our fauna. In order to serve for both filiform and pectinate antennæ, the table has to be practically double. Many characters which would be practicable for separation of filiform antennæ, either become obliterated or are seen with such difficulty when the forms become pectinate, that other separation characters must be found. In many cases also, two forms may be very unlike in appearance and even in structure, but at the same time be very difficult to distinguish by means of a description. The following table is constructed for the classification of the antennæ of males, but in most cases it will serve for the females also. The characters used are selected because they are what seemed the best recognition characters and not because they best represent the most essential differences in structural features.

THE FRENULUM-CONSERVERS.

A. Hairs of second type absent, or but little developed.
  B. Antenna filiform.
    C. Hairs of third type absent; or, if present, with no definite arrangement
      D. Cones large and on many segments.
        E. Scape large, twice the diameter of pedicel...CYMATOPHORIDÆ.
        EE. Scape small, but little larger than pedicel.......GEOMETRINA.
      DD. Cones small, and on few segments..................THYRIDIDÆ.
    CC. Hairs of third type inserted regularly.
      D. In a single row along the distal and proximal edges of ventral expansion.......................................GEOMETRINA.
      DD. In a semicircle opening ventrad (see Figs. 46 and 50).
        E. Ventral expansions shortening ventrad, not equal to the segment in length....................................NOTODONTIDÆ.
        EE. Ventral expansion not shortening ventrad, equal to the segment in length, so as to cause the end of the clavola to be recurved. SPHINGIDÆ
  BB. Antenna pectinate.
    C. Ventral expansion of the segment very large, extending ventrad of the bases of the pectinations........................SPHINGIDÆ.
    CC. Ventral expansion not extending far ventrad of the bases of the pectinations.
      D. Single hair of second type near middle of dorsal aspect of pectinations of the cephalic side..........................DREPANIDÆ.
      DD. Without hair of second type as in D.
        E. Cones on ventral aspect of shaft, not on pectinations.
          F. Pectinations on distal half of segment..........GEOMETRINA.
          FF. Pectinations on proximal half of segments........DIOPTIDÆ.
        EE. Cones at apex of pectinations, or beginning a migration out upon them.
          F. Clavola pectinate to distal end................NOTODONTIDÆ,
          FF. Clavola filiform at distal end..................GEOMETRINA.

AA. Hairs of second type present and well developed.
  B. Antenna filiform.
    C. Hairs of third type absent.
      D. Some hairs of second type on ventro-distal edge of segments. GEOMETRINA.
      DD. Hairs of second type not present as in D..........AGARISTIDÆ.
    CC. Hairs of third type present.
      D. Hairs of third type without definite arrangement.
        E. Hairs nearly straight, segments of usual shape........ARCTIIDÆ.
        EE. Hairs strongly curved, segments swollen, almost subglobose. LITHOSIIDÆ.
      DD. Hairs of third type inserted in rows, usually on the compressed ventral expansion in a semicircle opening ventrad.
        E. Ventral expansion narrow and slightly compressed.GEOMETRINA.
        EE. Ventral expansion large and usually compressed....NOCTUIDÆ.
  BB. Antenna pectinate.
    C. Pectinations relatively short.
      D. Scape large, twice the diameter of pedicel............NOCTUIDÆ.
      DD. Scape small, little larger in diameter than pedicel....ZYGÆNIDÆ.
    CC. Pectinations long and well developed.
      D. Cones small, or apparently wanting................PERICOPIDÆ.
      DD. Cones easily seen.
        E. Cones on shaft, or, if on pectinations, the latter have a single, strong hair of second type directly at the apex.
          F. Pectinations of cephalic and caudal sides subequal. GEOMETRINA.
          FF. Pectinations of caudal side longer...............ARCTIIDÆ.
        EE. Cones on pectinations, the latter with two strong hairs of second type at the apex.
          F. Cones very short..............................ZYGÆNIDÆ.
          FF. Cones large..............................LYMANTRIIDÆ.

The extent of my study and the limits of this thesis will not permit me to discuss each family of the Frenulum-conservers, but certain features are especially worthy of note. The evidences presented by antennal structures which might point to some relationships different from those shown in the classification of Professor Comstock are as follows: The antennæ of the Cymatophoridæ and the Thyrididæ seem to be closely related, and neither of them are widely separated from the higher forms of the Pyralidina. The antennæ, therefore, would seem to indicate a lower position for these families than that now assigned them. The antennæ of the Dioptidæ are very close to those of the Notodontidæ. The pectinations are more highly developed in the former, but the cones have not even begun to migrate along the pectinations. Instead of that, they are situated upon slight ventral elevations of the segments between and a little cephalad of the bases of the pectinations. In the Notodontidæ, the

cones have begun to migrate as in *Nerice bidentata*, where they have only reached a point near the bases of the pectinations, or they have already reached the apex as in *Cerura cinerea*, or *Icthyura inclusa*. The antennæ of the Noctuidæ, Lymantriidæ, Agaristidæ and Pericopidæ, are very similar in structure. There is a closer relation between the Noctuidæ and the Agaristidæ and between the Lymantriidæ and the Pericopidæ than exists in any other arrangement of the families. The Pericopidæ also present many points of resemblance to the Zygænidæ, especially to the more generalized forms. The Zygænidæ, however, seem to be most closely related to the Pyromorphidæ among the Generalized Frenatæ. Without any doubt, they belong where they are placed, high up among the Frenulum-conservers; therefore, I believe they are the ends of the branch, which, at an earlier time, gave rise to the Pyromorphidæ. Certain of the Deltoid Noctuids exhibit a strong resemblance to the Pyralids. They are of a higher type of structure however. One group, including *Herminia*, *Pityolita*, *Zauclognatha*, *Renia*, etc., have a peculiar modification near the middle of the clavola, which at once suggests the condition of things in *Desmia funeralis*. In *Herminia morbidalis* there are simply a couple of spurs on the ventral part of a segment. The greatest development is reached in *Renia restrictalis*. Fig. 28 represents this highly specialized organ in this species. The antennæ of the Sphingidæ resemble, in some features, those of the Notodontidæ and the Noctuidæ, but they are probably most closely related genetically to the Sesiidæ, and are representatives of a later development from the same branch. The Sphinx antenna shows as high a degree of specialization in certain directions as any of the moths. The Saturniina have more complicated pectinations, but that kind of a development is particularly adapted to their conditions of life. Among the swiftly flying Sphinxes such antennæ would be unwieldy and very liable to injury. Here we find a specialization much better fitted for habits of swift flight. Instead of long and numerous pectinations, we find greatly developed ventral expansions. The antenna of *Daremma undulosa* is a good example of the type; Fig. 46 represents one of the segments of the clavola. The scape is short and very stout; the pedicel also is short and stout, and is especially well supplied with the peculiar sense apparatus common to all forms; the clavola is large, and its shaft is heavier than in any other Lepidoptera; it is well protected by an abundance of scales on the

dorsal aspect, and it bears on its ventral aspect wide expansions, considerably compressed. These have hairs of the third type arranged on their sides in a semicircle with its opening directed ventrad. Within the semicircle is an abundance of pits and rods. The ventral expansions are as long as the segments which bear them, and near the apex of the clavola, where the shaft is smaller in diameter, they cause it to be more or less recurved, as we find it among the Hesperiina. In some of the pectinate forms, *e. g.*, *Smerinthus geminatus*, the ventral expansions are well developed and extend far ventrad of the bases of the pectinations. Such forms are found among those members of the group which are not so swift in flight as the other Sphingidæ.

The evidence of the antennæ in all these cases just noted is neither clear enough nor strong enough in itself to warrant any change in the classification, but it may suggest the direction of work on other organs. For the relationships of the larger groups, I do not believe the antennæ furnish as good guides as do other organs. For, while they are subject to great variation by reason of the peculiar habits and environment of the particular genus or species, they do not afford a sufficiently large basis for variation to leave a stable and constant ground-work for the tracing out of the paths by which the specializations are brought about. In smaller groups they are of great value. The best example of this is perhaps to be seen among the Saturniina in the Frenulum-losers. They are often of value also when other organs seem to be constant in a number of forms, *e. g.*, in the Noctuidæ, Agaristidæ, Pericopidæ and Lymantriidæ, the wing structures are pretty constant, but the antennal structures show considerable variation and afford characters to distinguish the groups.

The Frenulum-losers.

The Frenulum-losers include the Saturniina, Lacosomidæ, Lasiocampidæ among the moths, and the superfamilies Hesperiina and Papilionina comprising the skippers and butterflies. The following table will serve to separate the antennæ of the males of this group.

THE FRENULUM-LOSERS.

A. Antenna pectinate.

B. Pectinations ventral.

C. Pectinations of at least the cephalic side not extending to the apex of the clavola .... SATURNIINA.

CC. Pectinations extending to the apex.

D. Pectinations scaled on dorsal aspect .... LACOSOMIDÆ.
DD. Pectinations not scaled .... LASIOCAMPIDÆ.
BB. Pectinations dorsal .... SATURNIINA.
AA. Antenna clavate or falcate.
B. Clavola usually prolonged beyond the club, segments with some ventral expansion, often causing a recurving of the clavola beyond the club .... HESPERIINA.
BB. Clavola not prolonged beyond the club, segments without appreciable ventral expansion .... PAPILIONINA.

The most generalized antenna of this group belongs to the family Lacosomidæ. It bears a close resemblance to the antenna of the Bombycidæ and the Lasiocampidæ. In all three families the pectinations are long and slender, and arise from the ventral aspect of the segments. They are abundantly supplied with hairs of the third type and have pits along the dorsal aspect, especially near the apex of the pectinations. In the Lacosomidæ the pectinations are scaled, and there are fewer pits along the dorsal aspect. A study of the antennæ alone would lead to the belief that the Bombycidæ were more closely related to the Lacosomidæ than to the other Saturniina. In fact, there is such a wide difference between the antennæ of the first and those of the last two families of the Saturniina, that the first family would not be placed in the same superfamily were the classification based on those organs. The superfamily as now constituted includes the Bombycidæ, Hemileucidæ, Citheroniidæ and Saturniidæ. The antennæ of the members of the group may be separated by the following table:

SATURNIINA.

A. Pectinations ventral, single pair to a segment .... BOMBYCIDÆ.
AA. Pectinations dorsal.
B. Single pair to a segment .... HEMILEUCIDÆ.
BB. Two pairs to a segment.
C. Distal portion of clavola filiform .... CITHERONIIDÆ.
CC. Clavola pectinate throughout .... SATURNIIDÆ.

The Bombycidæ are the least specialized of the Saturnians, and probably represent a branch which long ago separated from the one that produced the other families. The pectinations are well developed, but they are ventral, and there is only a single pair to a segment. The pectinations are well supplied with hairs of the third type, and the shaft also bears them for the width of the space between the bases of the pectinations. A rather unexpected fact is that the antennæ of the female are nearly as well developed as those

of the males, while in most of the other Saturniina they are much less specialized.

The Hemileucidæ exhibit a line of development distinct from that of the Bombycidæ on the one hand in having the pectinations dorsal instead of ventral, and from the Citheroniidæ and Saturniidæ on the other in having a single pair of pectinations to a segment. Thus it appears that they belonged to the branch which produced the latter families after it had separated from the branch giving rise to the Bombycidæ.

The Citheroniidæ and the Saturniidæ have followed the same line of development in that they both have two pairs of dorsal pectinations to a segment. The first family has not progressed so far as the second; its members do not have their antennæ pectinate throughout. The antennæ of these families show a high degree of development also in the arrangement of the hairs of the third type. The spaces between the pectinations are nearly filled by long, interlacing hairs, which are regularly arranged in a distinct line of from two to three rows extending continuously from the apex of one pectination along the dorso-lateral surface of the segment to the apex of the other pectination of the same side. Fig. 54 represents the arrangement in *Dryocampa rubicunda*. Still another feature showing remarkable development of sense-organs is exhibited in the higher forms, especially in *Tropœa* and *Samia* of the Saturniidæ. This is the multiplication of cones. While in nearly all other moths cones are limited to one or at most two to a segment, we here find them literally heaped up on the ventro-distal edge of the segments of the distal portion of the antennæ; and on the pectinations also there are often several either at the apex or along the pectination at various intervals. Fig. 7 shows this condition in the antenna of *Tropœa luna*.

The family Saturniidæ is interesting in the series of form it presents. The genera *Coloradia, Automeris, Callosaturnia, Tropœa, Telea, Callosamia, Philosamia* and *Samia*, present a regular and progressive series. The following table will serve to separate the antennæ of the members of this family:

SATURNIIDÆ.

A. Antennæ of female with single pair of pectinations to a segment.
  B. Antennæ of male with distal pair of pectinations shorter than the proximal.
    C. Distal pair not more than half the length of the proximal... Coloradia.
    CC. Distal pair but little shorter.............................. Automeris.

BB. Antennæ of male with distal and proximal pairs of pectinations subequal. **Calosaturnia.**

AA. Antennæ of both sexes with two pairs of pectinations to a segment.

B. Proximal and distal pairs subequal in male, distal pair shorter in the female.

C. Distal pair of female very short, without hairs of the second type. **Telea.**

CC. Distal pair of moderate length with hairs of second type..... **Tropæa.**

BB. Proximal and distal pairs subequal in both sexes.*

C. Distal pair of pectinations of female shorter than, or only equal to, the proximal on the proximal segments.

D. Distal pair wanting in a few distal segments............ **Callosamia.**

DD. Distal pair present, at least in rudiments, to the distal end... **Samia.**

CC. Distal pair of pectinations of female longer than the proximal on the proximal segments.............................. **Philosamia.**

There is a gradual progression in complexity of development from *Coloradia* on the one hand, to *Samia* or *Philosamia* on the other. The females of *Coloradia, Automeris* and *Callosaturnia,* have a single pair of pectinations to a segment, while those of the other genera have two pairs. The males of the first two genera have the distal pair shorter, while the other have the two pairs subequal. There is also a gradual increase in both sexes from one end of the series to the other in the number and position of the cones. In *Samia* there is not only an abundance on the shaft, but many are on the pectinations of the distal portion of the clavola. There is some doubt as to whether *Samia* or *Philosamia* should be considered the higher form. The male *Samia* is more highly developed than the male *Philosamia;* but on the other hand, the female *Samia* is less developed than the female *Philosamia.* I believe that now *Samia* is the higher form, and that it has outstripped *Philosamia* in specialization in comparatively recent times. If the females lag behind the males, as seems most probable, the condition we find in the two genera would indicate that the male *Philosamia* has been long enough fixed to allow the female to approach it in specialization; while in *Samia* the male is even now progressing in complexity, and the female has not had time to approach it in development. There are many indications in the antennæ of *Samia* which point to its recent or even present progress. The pectinations are not well established in form and position; the cones are variable in position; even the segmentation is more or less indefinite in portions of the clavola.

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* The genus *Saturnia* belongs somewhere in this section. It is represented in the United States by a single rare species, *S. galbina*, and no specimen is at hand for study. The descriptions of the insect are too indefinite on points relating to the antennæ to be of any value, and it is necessary, therefore, to omit this genus from the table.

The Hesperiina and Papilionina are widely separated from the other Lepidoptera. The antennæ show that they, with the other Frenatæ, probably branched off from the Jugatæ very early. The character of the chitinous surface of the clavola allies them to the Frenatæ and at the same time the absence of cones in all forms shows that they branched off from the other Frenatæ before the origin of those organs. That the cones have been present, and have subsequently disappeared in all skippers and butterflies, is scarcely conceivable; that these organs have originated many times in the other Frenatæ is equally difficult to believe; we must conclude, therefore, that the cones originated early in the history of the Frenatæ, but that the Hesperiina and Papilionina separated from the Frenate stem before that origin. It is certain also that the Hesperiina and Papilionina separated from a stem-form common to the two. The ventral expansion producing the hook in so many members of the former superfamily is probably a development brought about after the separation took place. Most forms of the Hesperiina have a less abrupt club than do the butterflies. The clavola thickens more gradually from the proximal end, and it is often produced in a tapering point at the apex beyond the club proper. In most other respects the antennæ of the two forms present many common characters. The Hesperiid antenna is not so highly developed as those of the other superfamily. Both in the organs they possess and in the structure of the whole antenna, they exhibit a lower degree of specialization. The antennæ are inserted far apart, while in the Papilionina they are nearer together. The recurved hook so characteristic in such forms as *Epargyreus tityrus*, Fig. 4, our most common large skipper, does not occur in all forms. *Megathymus yuccæ*, another skipper of about the same size, but belonging to another family, lacks the hook, and there is only a slight curving of the end of the clavola, not more than is seen in some of the butterflies. In such forms, however, the ventral expansion is a feature which distinguishes them from the Papilionina.

The Papilionina includes the Papilionidæ, Pieridæ, Lycænidæ and Nymphalidæ. The Papilioninæ represents one line resulting from a dichotomous division of the stem-form of the Papilionina, and the three other families represent the other. The members of the subfamily Papilioninæ have developed a type of antenna quite different in some respects from that of the other forms. This confirms one of the most important changes made in the older classifications by

that of Professor Comstock--the separation of the Pieridæ from the Papilionidæ and association of them with the Nymphalidæ and Lycænidæ, while the Papilionidæ are left standing alone, except for the few almost archaic forms representing the Parnassians. Instead of scales and pits along the clavola as in the Nymphalidæ, or scales alone as in most of the members of the other families, there are in the Papilioninæ no scales distad of the first segment of the clavola, but there is an abundance of short hairs or rods which no doubt serve as sense organs, and possibly serve to compensate for the scarcity of well-developed pits of the usual type. The sense organs are scattered over the whole surface of the clavola with considerable regularity, and the lack of scales is doubtless due to their large development. In the Parnassiinæ we find the same short hairs or rods, but instead of extending over the whole surface of the clavola, they are confined to a more limited area along the distal portion. The Parnassians are doubtless nearer the stem form of the Papilionina than are the Papilioninæ. There are only four species, comprising a single genus, in the fauna of North America, and from their general structure they are regarded as a not very highly developed group. They have a thick covering of scales over the clavola, at least on the dorsal aspect, but the presence of the short hairs allies them to the Papilioninæ and separates them from the other families of butterflies. The antennæ of the Papilionidæ, then, indicate that they are distinct from the other butterflies, and that they are less highly specialized.

I am unable to find any definite characters in the antennæ themselves which are constant for the separate families, and which will separate the Pieridæ, Lycænidæ and Nymphalidæ. The Pieridæ, however, differ from the Lycænidæ in the insertion of their antennæ. In the former the antennæ do not infringe upon the eyes, while in the latter family, at least, the sockets do encroach upon the eyes. The Nymphalidæ have the most highly organized antennæ of all the butterflies. They are abundantly supplied with well-developed pits. The clavola has pits upon the ventral surface even to the proximal segment in some forms, and there are other indications that these forms express the highest antennal development among the butterflies.

It would perhaps be futile to compare the antennæ of the skippers and butterflies with those of the moths. There is a wide difference between the structure and the organs of the antennæ of two such

extreme forms as *Samia cecropia* and *Euvanessa antiopa*, but that each is best adapted to the other structures and to the life habits of the possessor, and is most efficient in supplying the needs of its existence, is perhaps unquestioned. *Samia cecropia* is chiefly nocturnal; even in closely allied diurnal forms, such as *Callosamia promethea*, vision appears to be of little service as a guide to the motion of the moth; and in such forms we find a higher degree of development in pectinations which bear an abundance of long sense-hairs of the third type. *Euvanessa* and the skippers and butterflies in general appear to have excellent vision, and in no case do they have pectinations or sense-hairs of the third type. The pits and rods, however, which are common to all families of the Lepidoptera, reach a higher development in *Euvanessa* than in *Samia*. We may assert, then, with a fair degree of confidence that the antennæ of the butterflies are more limited in their functions, but that within the limits of their scope they are more efficient.

SUMMARY.

The character of the subject of this thesis makes it difficult to summarize the results of the work. The more important features, however, may be noticed under the following numbers:

1. Muscles in the head move the scape; muscles in the scape move the pedicel; distad of the scape no muscles have been demonstrated, and the clavola is therefore capable of motion in itself only when acted upon by some external force causing a flexure and a subsequent extension.

2. Besides organs for protection, there are at least six types of sense organs situated in the antennæ, and all but one are developed from a simple sense-hair inserted at the ectal end of a pore-canal through which it is connected with a multinuclear sense-cell.

3. The antennæ doubtless function as sense organs of touch, smell and hearing, although those senses are not subject to the same limitations as in the higher animals and may be considerably different in their range of perception.

4. The antennæ show that all Lepidoptera are descended from one primitive stem form, of which we may predicate the more essential features of structure.

5. The evolution of ventral expansions, of pectinations, of the chitinous surface, of the sense organs shows an increasing differentiation of structure following the demand for increasing specialization of function.

6. In the more essential features, the evidence of the antennæ of all the families of the Lepidoptera confirms the provisional classification based upon the wing structures, though in a number of cases it indicated a change in the relationships of some of the families. These are indicated in the chapter on the discussion of the families.

CONCLUSION.

The work carried on upon the antennæ of the Lepidoptera proves that these organs are worthy of more extended study. Aside from the great interest which attaches to them as the most specialized sense organs, their value as records of the descent of families is very considerable in taxonomic work. In the determination of the relationships of the larger groups, they do not furnish as good guides as some of the larger organs, for while they are subject to great variation, they do not afford a sufficiently large basis for variation to leave a stable and constant ground-work for the tracing out of the paths by which the specializations are brought about. As supplementing the evidence of the wings they are valuable. This thesis has dealt only with the relationships of families and superfamilies, but there is a large field for work within these groups, and in many cases the antennæ will be found most important in taxonomic work. Owing to the difficulty of observation and the necessity for especial preparation, they afford few characters which would be practicable for recognition characters in ordinary systematic work, but for the more careful and painstaking work of the study of relationships they are of great value.

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DESCRIPTION OF FIGURES.

The figures were drawn by the author with a camera lucida and a Leitz microscope, and a scale from a Ewell stage micrometer was drawn by the side of the figure. All side views are placed on the page with the distal end towards the left. The same reference figures and numbers are used throughout.

Reference Figures and Numbers.

1.—Sense-hair of first type.
2.—Sense-hair of second type.
3.—Sense-hair of third type.
4.—Pit and rod.
5.—Cone.
6.—"Johnston's Organ."
ac.—axis-cylinder.
c.—sense-cell.
c. e.—compound eye.
ch.—chitin.
cl.—clypeus.
d. c.—dermal cell.
ep.—epicranium.
ge.—gena.
l.—labrum.
m.—muscle.
md.—mandible.
me.—membrane.
mx.—maxilla.
n.—nerve.
n. tr.—nerve-trunk.
oc.—occiput.
p.—pedicel.
pf.—pilifer.
pg.—postgena.
pl.—palpi.
r.—rod.
sc.—scale.
sc. c.—scale-cup.
sce.—scape.
su.—clypeal suture.

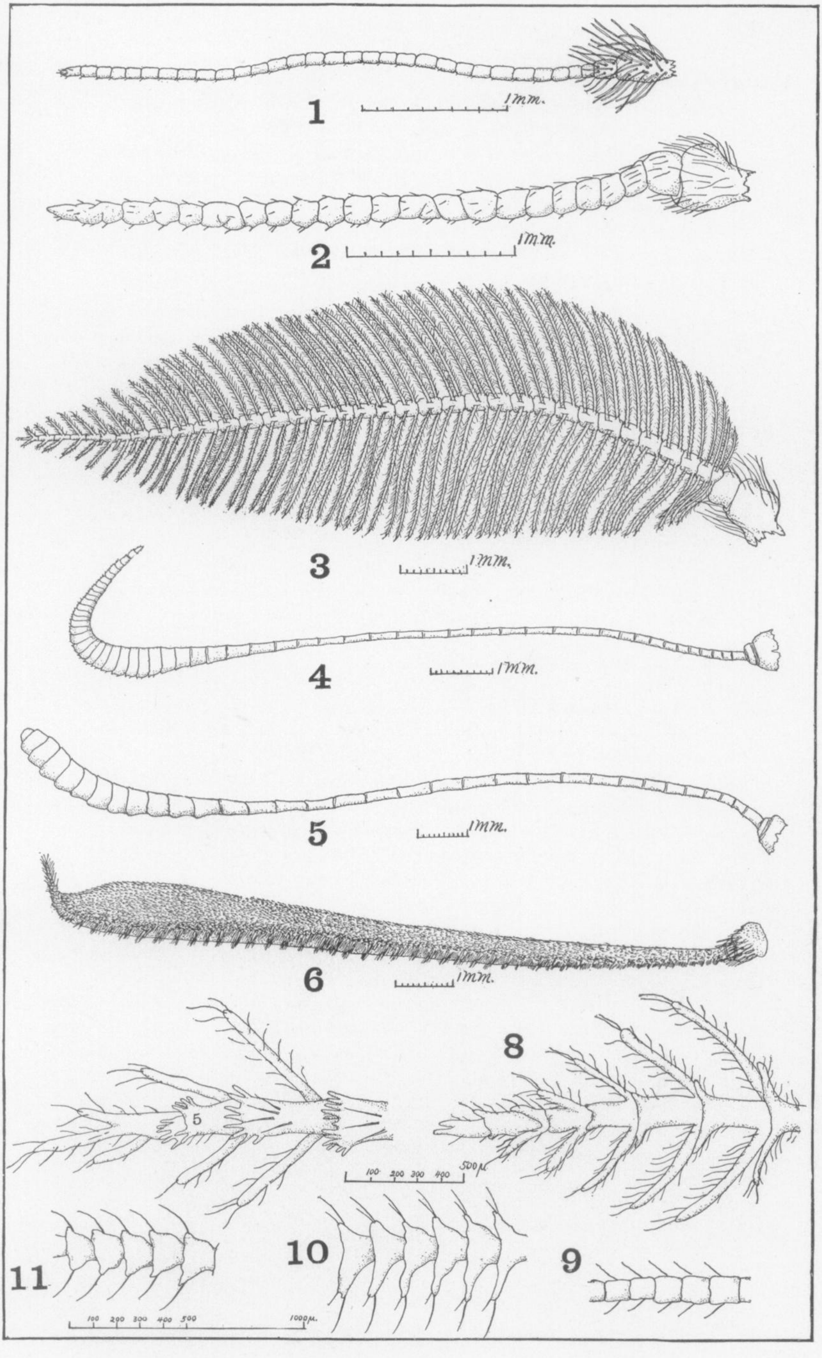
LIST OF FIGURES.

1. Antenna of ♂ *Micropteryx semipurpurella*, cephalic aspect.
2. Antenna of ♀ *Hepialus argentata*, cephalic aspect.
3. Antenna of ♂ *Philosamia cynthia*, dorsal aspect.
4. Antenna of ♂ *Epargyreus tityrus*, cephalic aspect.
5. Antenna of ♂ *Papilio polyxenes*, cephalic aspect.
6. Antenna of ♂ *Hemaris thysbe*, cephalic aspect.
7. Apex of antenna of ♀ *Tropæa luna*, ventral aspect; 5, cones on ventro-distal edges of segments.
8. Apex of antenna of ♂ *Automeris io*, dorsal aspect.

9, 10, 11. Portions of antenna of a ♂ *Feltia subgothica*, ventral aspect; 9, near apex; 10, near middle; 11, between 9 and 10.

12. Part of transection of clavola of ♂ *Callosamia promethea*, showing sense-hairs of third type.
13. Part of transection of clavola of ♂ *Callosamia promethea*, showing sense-hairs of first type.
14. Part of longisection of clavola of ♂ *Callosamia promethea*, showing sense-hair of second type.
15. Part of transection of clavola of ♂ *Callosamia promethea*, showing pit and rod.
16. Part of transection of scape of ♂ *Callosamia promethea*, showing insertion of scales.
17. Transection showing chitinous parts of pit and rod in a ♂ *Pyrameis cardui*.
18. Part of longisection of segment of clavola of ♂ *Callosamia promethea*, showing cone at ventro-distal edge.
19. Ventral half of longisection of scape and pedicel of ♂ *Callosamia promethea*, showing "Johnston's Organ" in the pedicel and the muscles in the scape.
20. Longisection of segment of antenna of ♂ *Callosamia promethea*.
21. Portion of clavola of ♂ *Crambus mutabilis*, cephalic aspect.
22. Portion of clavola of ♂ *Catocala cerogama*, cephalic aspect.
23. Transection of clavola of ♂ *Callosamia promethea*.
24. Portion of clavola of ♂ *Renia restrictalis*, cephalic aspect.
25. Portion of clavola of ♂ *Phryganidea californica*, ventral aspect.
26. Dorso-cephalic aspect of denuded head of ♂ *Sphinx chersis*.
27. Portion of clavola of ♂ *Zeuzera pyrini*, ventral aspect.
28. Proximal portion of ♂ *Saluda asperatella*, caudal aspect.
29. Middle portion of clavola of ♂ *Desmia funeralis*, caudal aspect.
30. Distal end of pectination of ♂ *Notolophus leucostigma*, showing character of chitinous surface and long sense-hairs of second type, dorsal aspect.
31. Central aspect of chitinous surface of pectination of ♂ *Notolophus leucostigma*.

32. Dorsal aspect of chitinous surface of ♂ *Automeris io.*
33. Lateral aspect of chitinous surface of ♂ *Daremma undulosa.*
34. Chitinous surface of ♂ *Pyrausta oxydalis.*
35. Chitinous surface of ♂ *Dichelia sulfureana.*
36. Chitinous surface of ♂ *Tinea dorsistrigella.*
37. Chitinous surface of ♂ *Cerura cinerea.*
38. Chitinous surface of ♂ *Hemileuca maia.*
39. Chitinous surface of ♂ *Papilio polyxenes.*
40. Fixed-hairs and scale-cups of ♂ *Micropteryx semipurpurella.*
41. Cone of ♂ *Samia cecropia.*
42. Cone of ♂ *Theretra tersa.*
43. Cone of ♂ *Megalopyge crispata.*
44. Cone of ♂ *Endropia hypochraria.*
45. Cone of ♂ *Pantographa lineata.*
46. Segment of clavola of ♂ *Daremma undulosa*, cephalic aspect.
47. Segment of clavola of ♂ *Pyrausta oxydalis*, cephalic aspect.
48. Apex of clavola of ♂ *Sannina exitiosa*, cephalic aspect.
49. Segment of clavola of ♂ *Sannina exitiosa*, cephalic aspect.
50. Segment of clavola of ♂ *Datana ministra*, cephalic aspect.
51. Segment of clavola of ♂ *Micropteryx seppela ?* cephalic aspect.
52. Segment of clavola of ♂ *Spilosoma virginica*, cephalic aspect.
53. Segment of clavola of ♂ *Micropteryx semipurpurella*, cephalic aspect.
54. Portion of clavola of ♂ *Dryocampa rubicunda*, cephalic aspect.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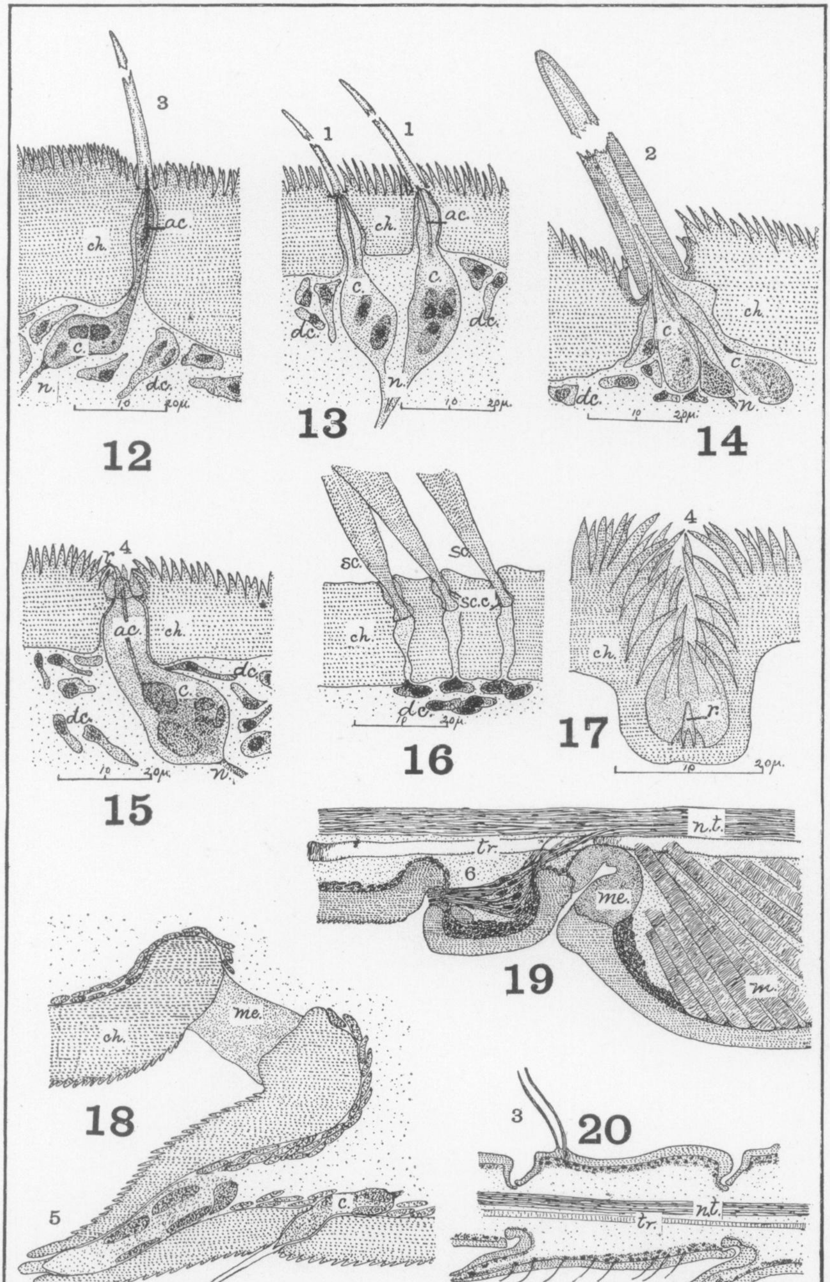
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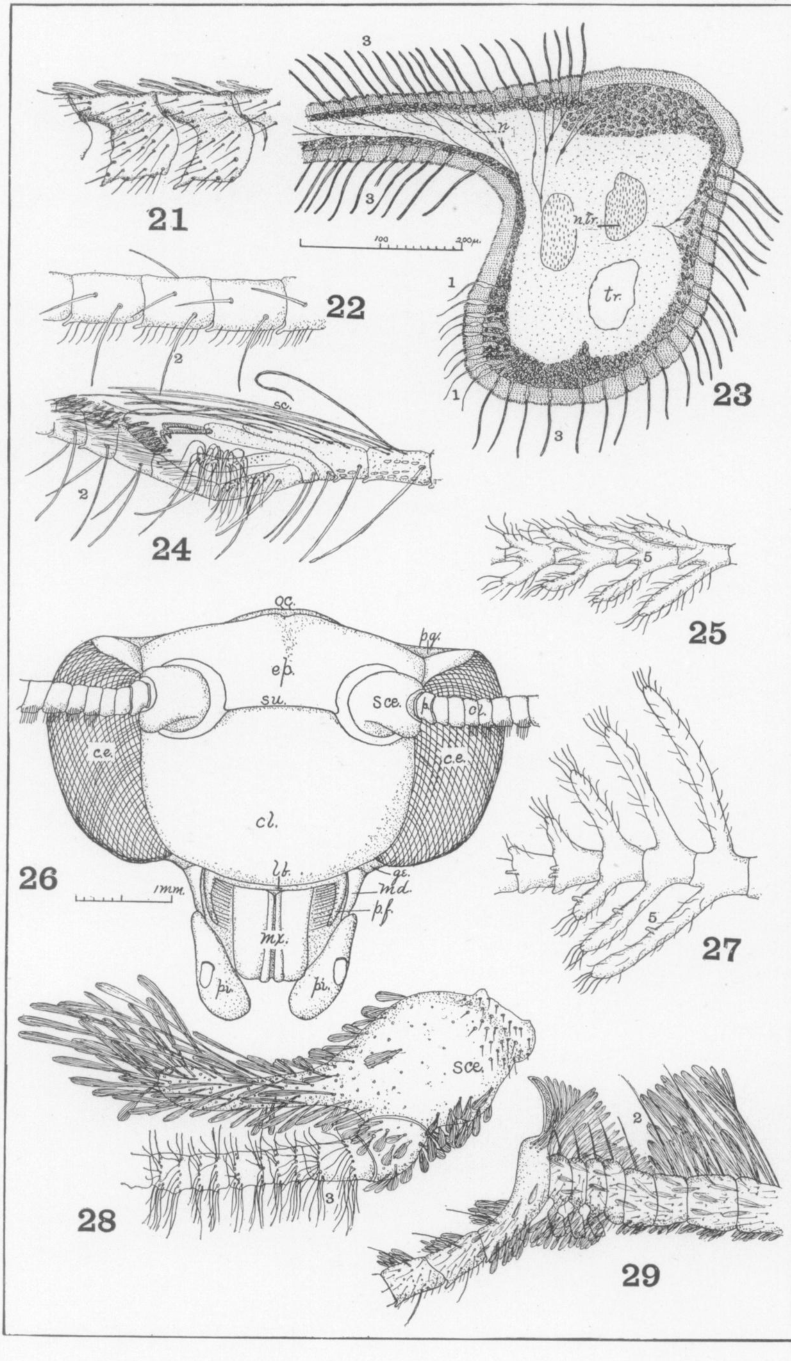

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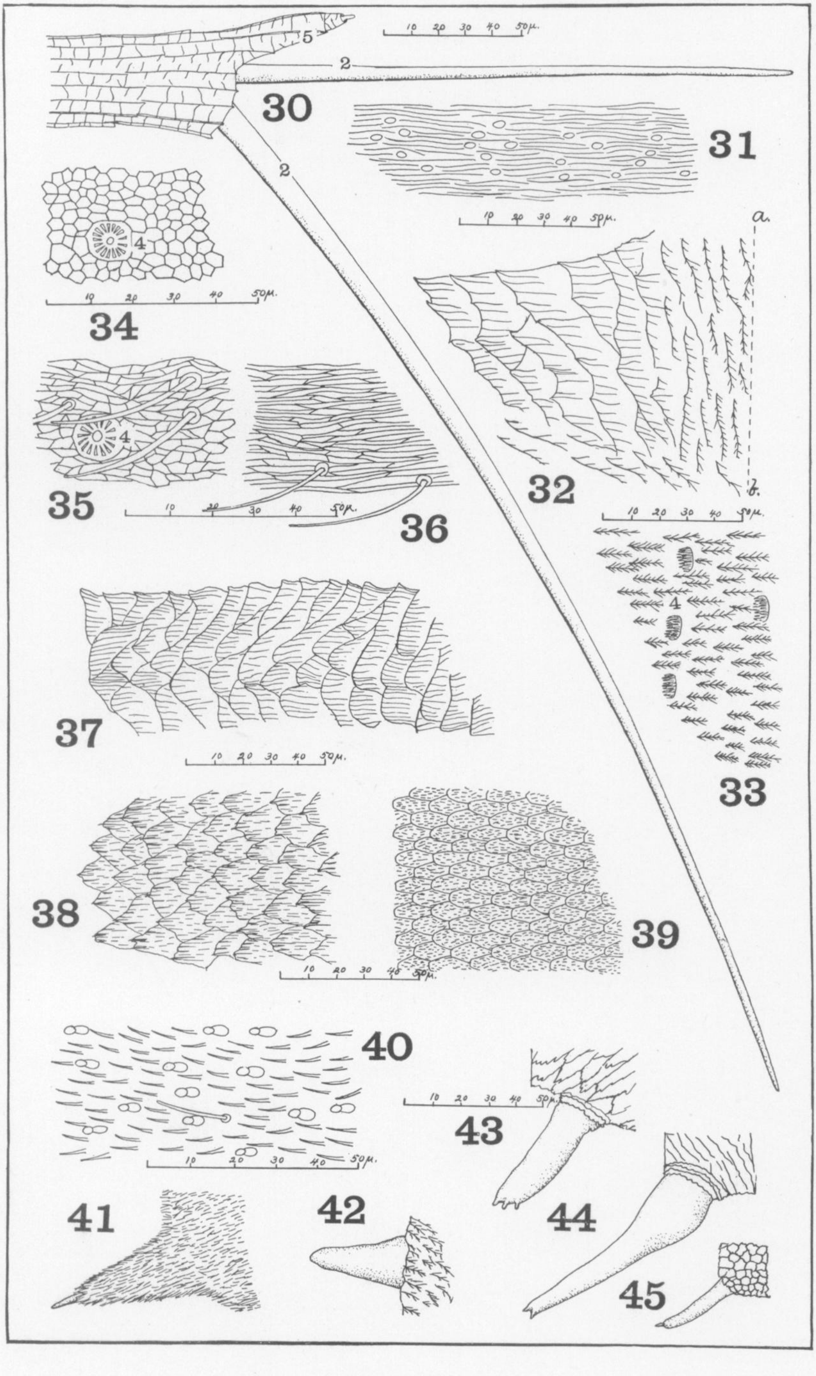
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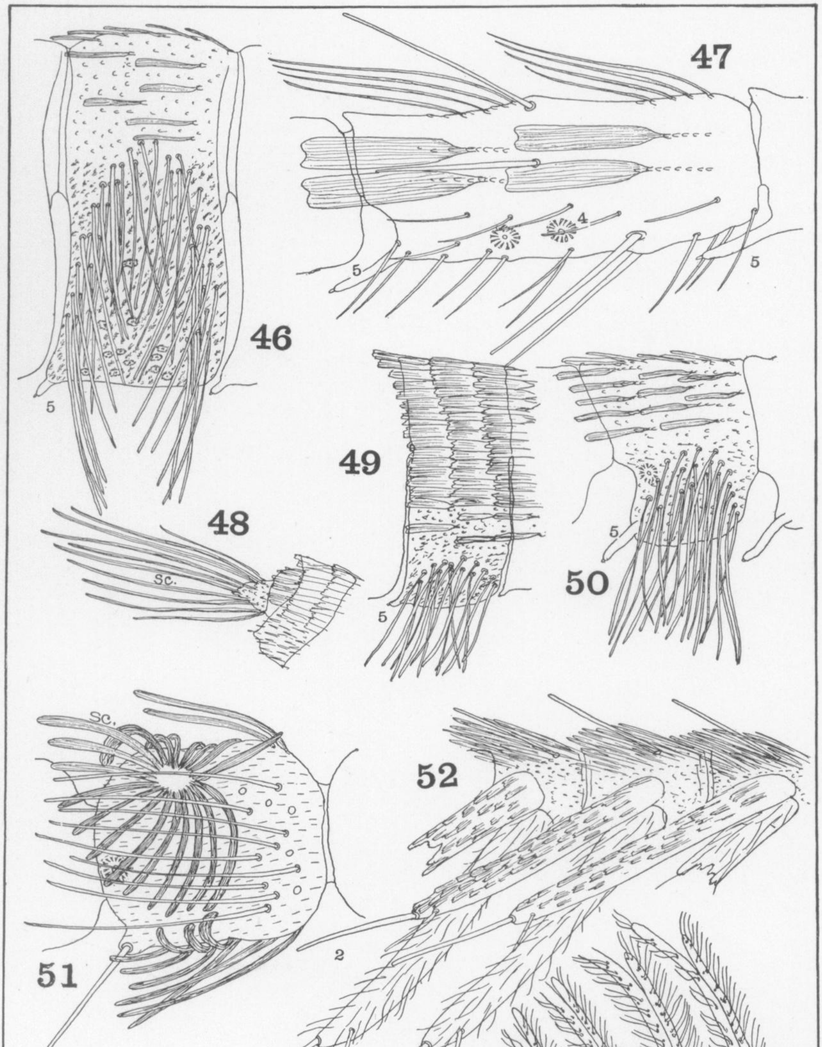
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